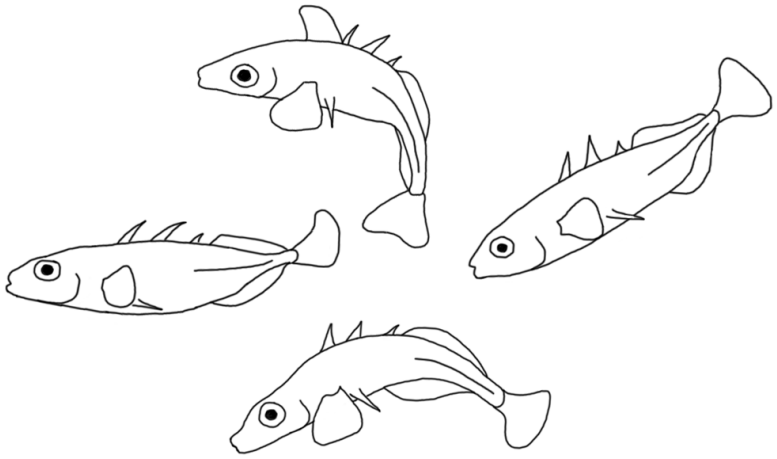
ANIMAL PERSONALITY and THE SOCIAL CONTEXT

The role of boldness and sociability variation in schooling fish



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Contents

Preface

This thesis is structured as a series of papers that are either published, in press or will be submitted for publication. I am the first author of all studies included in this thesis, and I formulated the hypotheses, designed and performed the experiments, analysed the data, and wrote the manuscripts. I was supervised by Dr Andrea Manica and received help with data collection and advice on experimental design, analysis, and writing from a number of colleagues who are included as co-author on the relevant papers or named in the acknowledgements. No part of this thesis has been submitted to any other university in application for a higher degree. The text does not exceed 60,000 words and no part has been submitted elsewhere in application for a higher degree or diploma. A list of other work that I published during my PhD but was not included in my thesis is listed in the Appendix.

Summary

Throughout the animal kingdom, individuals often differ consistently from one another in how they cope with their environment. In particular, consistent behavioural variation, known as animal personality, is a substantial driver of a range of important ecological and evolutionary processes. As most animal species are social for at least part of their lives and group living is common, a crucial link between personality and the social context may be expected. In this thesis I systematically investigate this link, using three-spined stickleback fish (*Gasterosteus aculeatus)* as my model system.

I begin by showing that fish vary consistently in their boldness and sociability, with only boldness being positively linked to food intake for fish at rest. This finding provides support for evolutionary theory that links personality variation to life-history strategies, and lays the basis for work related to the social context. I continue by investigating how the social context may modulate personality variation and show that short contact with a social group may have carry-over effects and obfuscate personality expression when individuals are alone. Next, I observed fish in different pairs over time and found that social experience from both the current as well as previous social contexts are integrated in the risk-taking and leadership decisions of individuals but also depends on their boldness type. This result provides support for the importance of social feedback in the expression of personality differences. I go on to demonstrate that, in a pair, bolder fish have lower social attraction, with positive effects on individual's leadership but negative effects on social coordination. Finally, by detailed tracking of the collective movements and group foraging of free-swimming shoals, I reveal boldness and sociability have complementary driving effects of on social structure, collective behaviour, and group functioning. Furthermore, I show that in turn the group composition determines the performance of individual personality types, providing a potential adaptive explanation for the maintenance of personality variation.

Taken together, these studies provide an integrated account of animal personality and the social context and highlight the presence of a feedback loop between them, with personality variation being a key driver of collective behaviour and group functioning but also strongly affected and potentially maintained by it.

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Chapter 1

General introduction

"One thing the early ethologists had in common was the wish to return to an inductive start, to observation and description of the enormous variety of animal behaviour repertoires and to the simple, though admittedly vague and general question: 'Why do these animals behave as they do?'"

Niko Tinbergen, 1963

For anyone who takes a careful look at our natural world it should be apparent that individual animals differ in their behaviour, even within an otherwise uniform population. One may observe ducks on a lake, for example, and see one pair of individuals in an aggressive encounter, some others swimming in close unison along the shore, a single individual far out on the water by itself, and some to actually approach you the human observer. Although perhaps interesting, these kind of behavioural differences are hardly surprising by themselves as they may be the direct result of stochastic differences in state, such as an individual's energy reserves. The attentive observer will have noticed, however, that individuals do not only often differ from one another in their behaviour, but that these differences are also often predictable over time.

From an evolutionary and ecological perspective, it is now very clear that inter-individual differences in behaviour are often highly structured, that is, consistent over time and correlated across contexts (Sih, Bell & Johnson, 2004a; Bell, Hankison & Laskowski, 2009). Furthermore, such consistent behavioural variation is omnipresent in natural populations and occurs in a wide range of animal taxa, including mammals, birds, reptiles and fish, as well as squid, spiders, and insects (Gosling, 2001; Sih et al., 2004b; Réale et al., 2007). Three-spined sticklebacks (*Gasterosteus aculeatus*), for example, differ consistently in their aggression towards intruders (Huntingford, 1976), great tits (*Parus major*) in their exploration of a novel environment (Dingemanse et al., 2002), common lizards (*Lacerta vivipara*) in their social attraction to conspecifics (Cote & Clobert, 2007) and social spiders (*Stegodyphus dumicola*) in their response to a potential predator (Pruitt & Keiser, 2014). Behavioural variation between individuals that is maintained through time and across contexts is termed 'animal personality' (Gosling 2001; also coping styles, Koolhaas et al. 1999; behavioural syndromes, Sih, et al 2004; temperament, Réale et al. 2007), with individuals termed to have different 'personality types'.

If inter-individual behavioural consistency is so prevalent, the question arises of how stable animal personalities actually are, what consequences they may have and why they exist in the first place. Most animal species are social for at least part of their lives, with group-living being a widespread phenomenon (Krause & Ruxton, 2002). Therefore a crucial link between animal personalities and the social context may be expected (Webster & Ward, 2011). My thesis is concerned with this exciting topic and addresses how the social context may affect personality expression, how personality differences may drive group behaviour, and to what extent the group composition determines individual success, thereby thus also potentially providing an adaptive explanation for the maintenance of personality variation. By focusing on the potential two-way interaction between animal personalities and the social context, I aim to develop an integrated and holistic view of personality differences, following the rich research tradition started by Niko Tinbergen in the 1960's.

1.1 Animal personalities

The study of personalities in non-human animals has a relatively short history. Although personality in animals had been tentatively described in early studies in the 1920's, such as Gerould's work on butterflies (1927) and Pavlov's work on dogs (1928), research on animal personalities was almost non-existent for most of the 20th century. Foremost, this was because traditionally researchers largely ignored intraspecific behavioural variation and treating it as non-adaptive variation around an optimal mean response (Wilson, 1998; Dall, Houston & McNamara, 2004). The first real landmark study on animal personality was published in 1976 when Felicity Huntingford demonstrated that individual sticklebacks that were active in an unfamiliar environment were also relatively aggressive towards conspecifics and bold towards a predator (Huntingford, 1976). It took until the mid 90's before further interest in the topic was stimulated, with the identification of a 'shy–bold continuum' among individual pumpkinseed sunfish (*Lepomis gibbosus*) (Wilson et al., 1993, 1994), and a link between consistent exploratory behaviour and the formation of behavioural routines in great tits (*Parus major*) (Verbeek, Drent & Wiepkema, 1994). At the beginning of the 21th century, animal personality had become a solid research topic and personalities described in over 64 species from a wide range of animal taxa (Gosling, 2001). A handful of reviews published in 2004 that focused on the ecological and evolutionary implications of personality helped the further acceleration of the field (Sih et al., 2004a,b; Dall et al., 2004).

Over the last 15 years, research on animal personalities has flourished, not only in Behavioural Ecology, but in numerous other fields including ethology, comparative psychology, evolutionary biology, animal welfare, and genetics (Gosling, 2001, 2008; Briffa & Weiss, 2010). A vast amount of research has been done on many aspects related to personality, reflected in the large number of reviews that have been written on the topic (e.g. Wilson, 1998; Koolhaas et al., 1999; Gosling, 2001; Sih et al., 2004a, 2012; Dall et al., 2004, 2012; Dingemanse & Réale, 2005; Carere & Eens, 2005; Bell, 2007; Réale et al., 2007, 2010a; Sih & Bell, 2008; Careau et al., 2008; Smith & Blumstein, 2008; Bell et al., 2009; Dingemanse et al., 2010; Schuett, Tregenza & Dall, 2010; Stamps & Groothuis, 2010b; Dingemanse & Wolf, 2010, 2013; Budaev & Brown, 2011; Conrad et al., 2011; Carter et al., 2013; Dall & Griffith, 2014; Mathot & Dingemanse, 2015). Crucial is, that personality differences are often heritable (Drent, van Oers & van Noordwijk, 2003; van Oers et al., 2005a), can be target of different forms of selection (Schuett et al., 2010; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010), and are substantial drivers of a range of important ecological and evolutionary processes (Stamps & Groothuis, 2010a; Sih et al., 2012; Wolf & Weissing, 2012). Personality has, for example, been shown to influence dispersal (Dingemanse et al., 2003; Cote et al., 2010), fitness (Dingemanse et al., 2004; Smith & Blumstein, 2008), reproductive success (Réale et al., 2000), disease transmission (Kortet, Hedrick & Vainikka, 2010) and habitat use (Wilson, 1998; Wilson & Mclaughlin, 2007).

1.2 Adaptive explanations

Explaining the evolution and maintenance of animal personality remains one of the major focus points of animal personality research. Not only do we have to explain why behavioural differences among individuals exist, we have to explain why such behavioural variation is maintained and consistent over time. Adaptive explanations of consistent behavioural differences are addressed by a large body of well-developed theory (e.g. Wilson, 1998; Dall et al., 2004; Dingemanse & Réale, 2005; Stamps, 2007; Réale et al., 2007; Wolf et al., 2007; Wolf, van Doorn & Weissing, 2008; Wolf, Van Doorn & Weissing, 2011; Biro & Stamps, 2008; Wolf & Weissing, 2010; Dingemanse & Wolf, 2010, 2013; Johnstone & Manica, 2011; Careau & Garland, 2012; Mathot et al., 2012; Wolf & McNamara, 2013; Sih et al., 2015; Mathot & Dingemanse, 2015). Here I limit myself to a brief sketch of such explanations and focus on how the social context may play a prominent role in this understanding.

Most theory explains personality as an adaptive outcome of underlying differences in state in combination with state-dependent behaviour (Dingemanse & Wolf, 2010; Wolf & Weissing, 2010; Sih et al., 2015). State is a broad term that generally refers to all those features of an animal that affect the costs and benefits of its behavioural actions (Houston & McNamara, 1999; Dall et al., 2004). It does thus, for example, not only refer to sex, age and energy, but also to experience, the ecological context, and recent behaviour of social partners. Beyond states that are inherently fixed, or very costly to change such as sex, when states are very labile, behavioural variation can be stabilised by various feedback mechanisms between behaviour and states (Sih et al., 2004a; Sih & Bell, 2008; Wolf et al., 2008), explained in more detail below.

One important feedback mechanism is based on experience and learning. In most cases, the more experience an individual has with a particular behaviour, the better that individual gets at performing that behaviour, making it advantageous for the individual to stick to the behaviour (Wolf & Weissing, 2010) and resulting in behavioural consistency (Wolf et al., 2008). Feedback may also arise based on behaviour-induced changes in an individual's condition (Stamps, 2007; Wolf & Weissing, 2012; Sih et al., 2015): initial differences in state among individuals result in differences in their behaviour, which act to reinforce the initial state differences and as a result stabilise the initial differences in behaviour (Rands et al., 2003; Stamps, 2007). One of the most widely recognised theories to explain personality differences via such positive feedback is the link between individual life-history and metabolic trade-offs (Wolf et al., 2007; Careau et al., 2008; Biro & Stamps, 2008; Careau & Garland, 2012). Central to this theory are growth-mortality trade-offs (Stamps, 2007; Biro & Stamps, 2008): individuals may show either a fast lifestyle associated with bold and aggressive behaviour and rapid reproduction, or a slow lifestyle with more cautious behaviour and delayed reproduction (Réale et al., 2010b).

Consistent behavioural differences can also be selected for directly when the behavioural responses of an individual are determined by the interactions with conspecifics and the

consistent responses that they make (Dall et al., 2004; Schuett et al., 2010; Bergmüller & Taborsky, 2010; Wolf et al., 2011). First of all, behaviour-induced changes that result in consistent behaviour can come about from social experience. For example, a model by Rands et al. (2003) demonstrated that in foraging pairs that have the possibility to hide, small initial differences in energy reserves result in initial differences in risk-taking behaviour, affecting the risk-reward trade-offs of their partner and consequently lead to differences in leading and following behaviour, with the individual with the highest energetic needs acting as leader.

Adaptive behavioural variation may also be maintained by negative frequency-dependent selection (Sih et al., 2004a; Wolf & Weissing, 2010) when fitness payoffs of behaviour depend on its frequency in the group or population as well as an individual's behavioural history (Wilson, 1998; Dall et al., 2004; Wolf et al., 2008). For example, if some individuals are responsive to environmental stimuli and others are unresponsive, those latter individuals can become consistent in their behaviour due to feedback via social experience (Wolf et al., 2008). This combination of positive feedback from experience and negative frequency-dependent selection can also work for more complex scenarios: the benefits of being in a particular social environment might depend on the frequency with which other individuals choose that environment. This mechanism can promote the coexistence of individuals in different social states, such as their spatial position within a group or their social role (Sih et al., 2015). Via social interactions and behaviour-experience feedback, individual differences in social roles or positions can thus potentially be reinforced, resulting in individuals to become specialised in a 'social niche', a collection of integrated and adaptive social, ecological, behavioural and life-history tactics (Bergmüller & Taborsky, 2010; Montiglio, Ferrari & Réale, 2013).

Although this thesis is not focused on the adaptive maintenance of personality variation, I touch on two potential processes that may help explain the adaptive nature of consistent behavioural variation. Namely, in Chapter 2 I test the prediction that boldness is positively linked to a higher food intake, even when individuals are at rest and do not have to make risk-reward trade-offs, which would support 'pace-of-life' theory (Biro & Stamps, 2008; Réale et al., 2010b). In Chapter 6 I investigate the role of personality variation in group functioning and how this may in turn affect individual performance, which can provide the basis for social feedback and frequency dependent selection that might maintain personality variation.

1.3 Personality and the social context

Since sociality is a central aspect of the lives of most animal species (Krause & Ruxton, 2002), we need to consider the social context to fully understand the causes and consequences of animal personality. By grouping and moving with others, individuals can gain benefits such as reduced predation risk, earlier predator detection and resource exploitation (Pitcher & Parrish, 1993; Krause & Ruxton, 2002), but with the costs of increased competition and predator

attraction (Krause & Ruxton, 2002). To ensure that individuals reap the benefits of grouping they coordinate their behaviour with other group members (Herbert-Read et al., 2011; Katz et al., 2011; Gautrais et al., 2012) to reach and maintain group coherence and consensus (Couzin et al., 2005, 2011), resulting in collective movements and decisions (Couzin et al., 2011; Miller, Garnier, Hartnett, & Couzin, 2013), and often the emergence of leaders and followers (Krause et al., 2000; King, Johnson & Van Vugt, 2009). Linked to these trade-offs and social dynamics, the social context is likely to affect individual personality expression. Furthermore, within-group variation in personality requires compromises. On the other hand, collective behaviour and leadership may be affected by personality variation and consequently drive the structure and functioning of animal groups.

Social influence on personality

The social context is one of the major modulating factors of individual behaviour (Webster & Ward, 2011; van den Bos, Jolles & Homberg, 2013) and can both restrict or enhance the behavioural responses of individuals (Webster & Ward, 2011). For example, individuals in a social group are often more active and exploratory (Gómez-Laplaza & Morgan, 1991; Webster, Ward & Hart, 2007), show more risk-taking behaviour (Magnhagen & Bunnefeld, 2009) and are less vigilant and attentive to novelty (Gómez-Laplaza & Morgan, 1986) compared to individuals that are alone.

Across social contexts, the behaviour of individuals is often rather plastic (van Oers, Klunder & Drent, 2005b; Webster et al., 2007; David, Cézilly & Giraldeau, 2011; Morand-Ferron, Wu & Giraldeau, 2011). Individuals thereby modulate their behaviour based on that of others (Reebs, 2000; Webster & Ward, 2011; Herbert-Read et al., 2012), as well as to the composition of the group (Magnhagen & Staffan, 2005), and the sex (Schuett & Dall, 2009; Piyapong et al., 2010) and personality (van Oers et al., 2005b; Magnhagen & Bunnefeld, 2009) of their group mates. For example, individual three-spined sticklebacks with a higher propensity to take risks when they are alone (bolder) are more likely to take risks when paired with a conspecific, but this is strongly dependent on the boldness type of their group mates (Harcourt et al., 2009; Nakayama et al., 2012a, 2013). As a result, in a social context, individual personality is in most cases only expressed to a limited extent (Webster et al., 2007; Magnhagen & Bunnefeld, 2009; Herbert-Read et al., 2012; Castanheira et al., 2013).

As a result of the modulating effects of the social environment, the behavioural variance amongst individuals tends to be reduced (Gómez-Laplaza & Morgan, 1986; Magnhagen & Bunnefeld, 2009; Herbert-Read et al., 2012). Furthermore, as personality types are often linked to differences in responsiveness and behavioural plasticity (Magnhagen & Bunnefeld, 2009; Wolf et al., 2011), such as shyer individuals behaving more flexibly across social contexts (Nakayama et a., 2012a,b), rank order differences in behaviour may often be obfuscated. However, in contrast to short-term effects of the social context, long-term exposure to a stable

social environment may actually increase behavioural variability and repeatability by positive feedback from experience via repeated interactions (Wolf et al., 2011; Laskowski & Bell, 2013; Laskowski & Pruitt, 2014).

It is clear that the social context may have large direct effects on personality. However, the crucial question remains whether experience of the social context may carry-over and modulate the personality expression of individuals when they are alone. Furthermore, to fully understand how social experiences affect personality expression and thereby influence the behavioural decisions of individuals, it is necessary to investigate how personality types are affected by current versus previous social contexts. These fundamental issues are addressed in Chapters 3 and 4 respectively.

Collective behaviour

The spectacular and complex patterns of collective behaviour exhibited by many group-living animals can often be explained by animals following simple rules (Couzin & Krause, 2003; Sumpter, 2006, 2010; Herbert-Read et al., 2011; Katz et al., 2011; Gautrais et al., 2012). However, the structure and functioning of social groups may be strongly affected by individual personality variation and the composition of the group (Harcourt et al., 2009; Webster & Ward, 2011; Aplin et al., 2014; Wolf & Krause, 2014; Farine, Montiglio & Spiegel, 2015). In particular 'sociability', the tendency of individuals to approach others, and 'boldness', the tendency of individuals to accept risks for potential rewards (Réale et al., 2007; Bell et al., 2009; Laskowski & Bell, 2014), may play important roles in the dynamics and functioning of animal groups.

From a theoretical viewpoint, variability in social attraction is predicted to result in more social individuals having more central positions and less social individuals featuring more in front of animal groups (Couzin et al., 2002; Conradt et al., 2009). Furthermore, since predation risk (Bumann, Krause & Rubenstein, 1997; Krause et al., 2000) and foraging benefits (Krause, Reeves & Hoare, 1998; Krause & Ruxton, 2002) are generally higher at the edge and in the front of animal groups, these positions are more likely to be occupied by 'needier' (Conradt et al., 2009) and thus potentially bolder individuals. As group movements are generally determined by individuals in the front of the group (Bumann & Krause, 1993; Krause et al., 2000), both variability in sociability and boldness may thus be expected to result in group leadership, and consequently to have large potential effects on group foraging dynamics (Krause et al., 1998; Krause & Ruxton, 2002). Differences in social attraction may potentially even be an expression of boldness, as individuals may lower their predation risk by staying close to others and responding more strongly to their behaviour (Krause & Ruxton, 2002).

Although research that investigates the role of animal personality in collective behaviour is still in its infancy, studies have already shown that boldness differences are linked to leadership (Harcourt et al., 2009; Kurvers et al., 2009), foraging dynamics and producer-scrounger roles (Dyer et al., 2009a; Kurvers et al., 2010b; Jolles, Ostojić & Clayton, 2013b;

Laskowski & Bell, 2014), and the social organisation of individuals (Pike et al., 2008; Croft et al., 2009; Aplin et al., 2013, 2014). In line with theoretical expectations, bold individuals typically lead and shy individuals mainly follow (Beauchamp, 2000; Ward et al., 2004; Harcourt et al., 2009; Kurvers et al., 2009; Nakayama et al., 2013). However, the link between boldness and leadership behaviour is strongly affected by the interaction dynamics among individuals (Harcourt et al., 2009; Nakayama et al., 2012a; Ward et al., 2013; Pettit et al., 2013), and individual differences in leading and following behaviour may be strongly enhanced or reduced by social feedback (Harcourt et al., 2009; Nakayama et al., 2012a). Bold individuals are more likely to discover foraging areas, while shy individuals are more likely to join others and 'scrounge' at already discovered patches (Dyer et al., 2009a; Kurvers et al., 2010b), depending on the associated risks (Jolles et al., 2013b). Furthermore, bold individuals are often less likely to shoal (Ward et al., 2004) and less responsive to the behaviour of their group mates (Croft et al., 2009; Harcourt et al., 2010a; Kurvers et al., 2010a; Nakayama et al., 2012a). This result is linked to the finding that in a collective context, bolder and more proactive individuals tend to have fewer and weaker social interactions (Pike et al., 2008; Dyer et al., 2009a; Aplin et al., 2013), while reactive individuals are more often positioned in the centre of the group (Aplin et al., 2014). Finally, personality differences may also drive the behaviour of the group as a whole, for example, group foraging and productivity may be driven by the boldness of keystone individuals (Pruitt & Keiser, 2014) or the boldness personality composition of the group (Dyer et al., 2009a; Keiser & Pruitt, 2014).

Surprisingly, little is still known about the role of sociability in collective behaviour. Nevertheless, the few studies that exist suggest this trait is an important factor in the dynamics of animal groups. Namely, more sociable individuals have a lower tendency to disperse (Cote et al., 2010), are more selective in their grouping decisions (Cote, Fogarty & Sih, 2012), and play a key role in group exploration (Brown & Irving, 2014), while food finding rates are positively affected by a more social group personality composition (Laskowski & Bell, 2014).

Together, these studies show that personality variation may have profound consequences for the collective movements, leadership, foraging dynamics, and social structure of animal groups. That leadership is not only strongly linked to boldness but also positively affected by social feedback may help explain the maintenance of this consistent behavioural variation. If that is the case, social feedback from previous social experiences may affect risk-taking and leadership behaviours in later social contexts. I test this prediction in Chapter 4. Furthermore, the existing literature suggests an indirect link between boldness and sociability may exist. In Chapter 5 I address the mechanistic role of social attraction in coordination and leadership behaviour and investigate its link with boldness in the context of collective behaviour.

Until now a major challenge has been to link individual behaviour to group-level outcomes. The exact mechanisms underlying how the various personality traits of an

individual may affect their behaviour in a group context, how these in turn may drive the behaviour of the group, and ultimately affect group functioning and success remain unclear. This comprehensive and exciting topic is the focus of Chapter 6.

1.4 Study species

I used the three-spined stickleback, *Gasterosteus aculeatus*, as my study species. This robust little fish is common throughout the northern hemisphere (Bell & Foster, 1994), shows remarkable variation in a whole suite of morphological and behavioural traits both across (Bell & Foster, 1994) as well as within populations (Huntingford & Coyle, 2010). In particular, sticklebacks have evolved traits that protect them against the wide range of predators to which they may fall prey (Reimchen, 1994). They possess bony armoured plates and dorsal and pelvic spines (Hoogland, Morris & Tinbergen, 1956), have cryptic body colouration that varies according to their habitat (Huntingford & Coyle, 2010) and spent considerable time under or near aquatic cover (Huntingford, Wright & Tierney, 1994). Outside the breeding season, sticklebacks form shoals, often with the same individuals (Huntingford & Coyle, 2010), which not only provide protection against predators, but also benefit the individual in terms of finding food (Pitcher & Parrish, 1993; Krause & Ruxton, 2002). Although the social structure of sticklebacks is fairly fluid and marked by fission-fusion dynamics (Ward et al., 2002; Croft et al., 2005), individuals often prefer to associate with familiar partners (Barber & Wright, 2001; Ward et al., 2002).

Their small size, robust behaviour and physique and tractability makes the three-spined stickleback ideal for carrying out highly controlled experimental studies of their behaviour (Huntingford & Ruiz-Gomez, 2009). Unsurprisingly, since Niko Tinbergen's early work (Tinbergen, 1951), the three-spined stickleback has been a key model species for ethologists, behavioural ecologists, evolutionary biologists, parasitologists and geneticists (Bell & Foster, 1994; Barber & Nettleship, 2010) and has helped address a wide range of the most exciting questions (Wootton, 1976; Bell & Foster, 1994; Gibson, 2005; Ostlund-Nilsson, Mayer & Huntingford, 2010). In particular, it has proven to be an excellent subject for investigating both the causes and consequences of personality differences as well as the dynamics of interactions within groups (e.g. Coolen et al., 2003; Ward et al., 2004, 2008; Bell & Stamps, 2004; Bell, 2005; Croft et al., 2005; Webster et al., 2007; Dingemanse et al., 2007; Ioannou, Payne & Krause, 2008; Pike et al., 2008; Harcourt et al., 2009; Nakayama et al., 2012a; Laskowski & Bell, 2014; Lacasse & Aubin-Horth, 2014). For example, relevant in the context of this thesis, three-spined sticklebacks show consistent variation in boldness and sociability (Ward et al., 2004; Harcourt et al., 2009; Laskowski & Bell, 2014), and both of these traits affect their group foraging dynamics (Ward et al., 2004; Webster et al., 2007; Ioannou et al., 2008; Laskowski & Bell, 2014). Furthermore, boldness influences the social organisation and interaction dynamics within groups (Pike et al., 2008) as well as leadership behaviour (Ward et al., 2004; Harcourt et al.,

2009; Nakayama et al., 2012a). Finally, their personality expression has been shown to be affected by the social context (Webster et al., 2007; Laskowski & Bell, 2013) and by associated social feedback (Harcourt et al., 2009, 2010b).

1.5 Thesis outline

The previous sections suggest that intricate links exist between personality and the social context, with large potential ecological and evolutionary implications. The aim of this thesis is to provide an integrated account of these links as well as their implications, described in five experimental chapters. I use a stepwise approach to address the potential two-way interaction between animal personality and the social context, as well as the potential adaptive explanations for personality variation. The role of aggressive and mating interactions are beyond the scope of this thesis and are not considered.

In **Chapter 2** I start by determining to what extent personality differences may be explained outside of any social context and address a prominent theory that provides an adaptive explanation for boldness variation by linking it to growth-mortality trade-offs (Stamps, 2007; Biro & Stamps, 2008). I provide support for this theory by showing that boldness but not sociability is positively linked to food intake, even for fish that are at rest and after accounting for differences in body size.

In **Chapters 3 and 4** I turn to the stability of behaviour and investigate how the social context may affect personality expression. Although it is already clear that the social context may have large direct effects on personality, in **Chapter 3** I show that relatively short-term social conditions can also have carry-over effects and influence personality expression even when fish are alone. In **Chapter 4** I investigated such carry-over effects in the context of social behavioural decisions of individuals and demonstrate that risk-taking behaviour and leadership roles are affected by social experiences from previous partners, and that this response depends on an individual's personality, with the personality of a previous partner affecting bold but not shy fish.

In **Chapter 5** I focus on the role of social attraction in the movements of pairs of fish and investigate its direct link with boldness. The existing literature seems to suggest that a negative link between sociability and boldness may exist, but the mechanistic role of sociability in the context of collective behaviour remains unclear. I demonstrate that an individual's social attraction is linked to both its own boldness as well as that of its partner, that it is negatively linked to leadership, but that it has a positive effect on the behavioural coordination of pairs of fish.

Until now a major challenge has been to link individual behaviour to group-level outcomes, especially with a focus on personality variation. In **Chapter 6** I used detailed individual tracking of free-swimming stickleback shoals to investigate the role of boldness and

sociability in the context of collective movements and group foraging. I not only show that boldness and sociability have complementary effects on the spatial positioning and leadership of individuals, but that these effects in turn drive collective behaviour and explain group functioning. I demonstrate how the complementary effects of both traits as well as the group composition ultimately determine individual success, which help explain the origins of behavioural differentiation and the maintenance of personality variation.

In **Chapter 7** I synthesise the main findings, discuss arising questions, and provide directions for future work.

Chapter 2

Food intake rates of inactive fish are positively linked to boldness in three-spined sticklebacks

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Abstract

It is now well known that fishes differ in personality traits such as boldness, aggression, and sociability, but how is this inter-individual variation maintained? One prominent theory places personality differences in the context of life-history strategies and a pace-of-life syndrome: bold individuals take more risks, linked to faster growth rates and higher energetic needs, leading to the prediction that they should also have higher food intake rates than shy individuals even when inactive. Here this idea was tested for the first time, using food-deprived three-spined sticklebacks *Gasterosteus aculeatus* at rest, and confirmed, as maximum food intake was positively linked to boldness, even after accounting for body size.

It is now well known that consistent individual differences in behaviour, referred to as animal personality, are ubiquitous across the animal kingdom (Réale et al., 2007; Dingemanse & Wolf, 2010; Sih et al., 2015). Personality differences have been shown to be linked to fitness, to affect population dynamics, and to have fundamental ecological and evolutionary implications (Réale et al., 2007; Wolf et al., 2007; Dingemanse & Wolf, 2010; Conrad et al., 2011). However, the major question remains why animal personalities exist in the first place.

One of the most prominent theories to explain animal personalities from an adaptive perspective is that they exist because of underlying individual differences in state (Dingemanse & Wolf, 2010; Sih et al., 2015), with the most widely proposed mechanism explaining personality differences in the context of broad life history strategies (Stamps, 2007; Wolf et al., 2007; Biro & Stamps, 2010), integrating behaviour into the concept of a pace-of-life syndrome (Réale et al., 2010b). Central to this theory is that differences in traits such as boldness and aggression may arise through growth-mortality trade-offs (Stamps, 2007; Biro & Stamps, 2008), effectively linking energetics with animal personality research (Careau & Garland, 2012). According to this view, individuals with high rates of growth and fecundity are expected to show physiological and behavioural adaptations associated with greater energy needs, such as higher rates of food intake and a greater tendency to take risks (i.e. bolder), both as a cause and consequence of their fast lifestyle (Biro & Stamps, 2008; Careau & Garland, 2012).

Empirical evidence is accumulating to support this theory: traits such as activity, aggressiveness and boldness have been found to positively correlate with growth, fecundity and other life-history traits (Biro & Stamps, 2008; Burton et al., 2011; Conrad et al., 2011; Careau & Garland, 2012), and are positively related to rates of food consumption (Biro & Stamps, 2008). For example, Ioannou et al. (2008) showed that pairs of three-spined sticklebacks *Gasterosteus aculeatus* L. 1758 that were quicker to leave refuge, took less time to explore a potentially risky environment and consumed more live prey than those that hid under cover for longer. In addition, individuals with higher growth rates and fecundity would also require higher-capacity 'metabolic engines' (Biro & Stamps, 2010), which is reflected by their higher resting metabolic rates ('RMR'; Huntingford et al., 2010; Burton et al., 2011; Martins et al., 2011). Therefore, even when not currently engaging in any energetically expensive activities, such individuals are predicted to have higher energy requirements and thus food intake (Biro & Stamps, 2010).

Here, for the first time, it is tested whether personality differences are linked to food intake rates when individuals are at rest and risk-reward trade-offs are kept at a minimum, providing a more mechanistic link between boldness and food intake compared to previous work focused on ecological consequences (e.g. Ioannou et al., 2008). Most variation in the food intake of inactive individuals is expected to be due to body size, with larger individuals eating more (Beukema, 1968; Allen & Wootton, 1984). Nevertheless, as boldness has been shown to positively correlate with growth and fecundity (Biro & Stamps, 2008; Careau & Garland, 2012),

and risk-taking behaviour with RMR (Killen, Marras & McKenzie, 2011), it was predicted that bolder individuals would have a higher maximum food intake than shyer individuals, even when at rest and after accounting for body size. In contrast, personality traits that may not be strongly linked to growth or fecundity, such as sociability, are expected to not affect maximum foraging rates when at rest.

To test these predictions, we randomly selected 96 *Gasterosteus aculeatus* from a wild stock which had been caught in tributaries of the river Cam, Cambridge UK and were socially housed in an environmentally controlled laboratory. During this time before the start of experiments (over 6 months), the socially-kept *G. aculeatus* were fed bloodworms (*Chironomidae* larvae) *ad libitum* at the end of each day. Individuals were individually photographed to measure their standard length (L_S, from tip of snout to caudal peduncle), which ranged from 3.06 to 5.25 cm (mean ± S.E. = 4.07 ± 0.04 cm). Mass (M) was estimated from total length (L_T; 5.13 ± 0.05 cm) based on L_T-mass relationship data of sticklebacks extracted from www.fishbase.org, using the formula $M = a \times L^b$ (a: 0.0068, describes body shape and condition; b: 3.28, describes isometric growth in body proportions) following Froese et al. (2014). This formula thus does not take into account any individual variation in other body measurements. The resulting body mass estimates ranged from 0.56 to 3.02 g (1.50 ± 0.05 g). After photographing, individuals were solitary housed in compartments (18.5 × 9.5 cm; 18 cm deep) that were lined with gravel and contained an artificial plant for cover. To minimise stress of isolation, compartments had perforated transparent Perspex walls that enabled the transfer of visual and chemical cues of seven conspecifics in neighbouring compartments. Each compartment contained a 2 cm-wide feeding dish at the plant cover so that individuals could feed while staying concealed under cover.

After 3 days of acclimatisation, *G. aculeatus* were first assessed for boldness, i.e. their willingness to take risks, and sociability, i.e. their tendency to approach others excluding aggressive behaviour (Réale et al., 2007). To quantify boldness, an experimental setup was used as detailed in Chapter 4 and 5. In short, individuals were placed in a rectangular tank (55 cm length × 15 cm width × 20 cm height) lined with sand in a slope ranging from a deep (15 × 10 cm; 13 cm depth), 'safe' area that contained an artificial plant for cover, to a shallow depth (3 cm) at the other side. Boldness was quantified as the amount of time an individual spent out of plant cover during the 30 min trial, with bolder individuals spending more time out of cover. To quantify sociability, individuals were placed in the larger middle compartment (30 cm width) of a tank (50 × 30 cm, 8 cm water depth) that was lengthwise divided by two transparent Perspex partitions. One of the two smaller side compartments (10 cm width) contained five conspecifics. Sociability was quantified by measuring the average distance of the focal individual from the compartment containing the conspecific shoal during a 15 min trial. The conspecific shoal was created by randomly selecting individuals from the stock tanks, and allowed to acclimatise to the compartment for 45 min at the start of each test day. The position

of the compartment housing the shoal was randomised every four trials, and after each compartment swap the shoal was allowed to acclimatise for 10 min before the start of the next trial. Eight individuals were tested in identical tanks simultaneously, and different conspecifics were used to form the shoal in each of the eight sociability-test tanks and for each test day. Test trials were video recorded from above and subsequently tracked using custom tracking scripts in Python 2.7.5 (see Chapter 6), providing detailed positional coordinates for each individual during each boldness and sociability trial. To standardise hunger levels, individuals were fed three bloodworms at the end of each day until all personality testing was finished.

To investigate the repeatability of behaviour, the key requirement of animal personality, individuals received two boldness sessions (on days 4 and 8 after individual housing) and two sociability sessions (on days 6 and 10). Based on the positional coordinates during the personality trials, it was found that individual *G. aculeatus* spent on average 27.9 ± 1.4% of their time out of cover (range: 0.0 - 62.8%) during the boldness test and were on average 47.9 ± 2.3 mm from the compartment housing conspecifics (range: 13.0 - 116.0 mm) during the sociability test. As individual fish ($n = 96$) were repeatable in the time they spent out of cover ($r_s = 0.41$, $p < 0.001$) and in their average distance from the shoal compartment ($r_s = 0.50$, $p < 0.001$), boldness and sociability scores were calculated for each individual by averaging their behaviour across the two test sessions for each trait. Boldness was not correlated with sociability ($r_s = 0.00$, $p = 0.989$) and neither personality trait correlated with L_S ($r_s = 0.11$, $p = 0.283$; $r_s = 0.10$, $p = 0.348$ respectively).

A week after personality testing, during which two fish had died from unknown causes, all individuals ($n = 94$) received a single bloodworm daily for three consecutive days to minimise stomach fullness and to make sure bloodworms would be consumed immediately when provided (see Beukema, 1968). Starting at 14:30 hours on the fourth day of food restriction, individuals' maximum food intake was measured by dropping five medium-sized bloodworms (12.7 ± 0.4 mg wet mass, based on 50 randomly selected worms) onto the feeding dish in each individual's home compartment. After 15 min, the number of bloodworms eaten was determined and five additional bloodworms were provided in the same manner unless some bloodworms remained uneaten. In the latter case, no additional bloodworms were provided during that round. If during a later round all bloodworms were eaten, an additional five were provided. Individuals were considered satiated if they did not consume any bloodworm for at least 30 min while bloodworms were still available on their feeding dish. As the maximum daily food intake may be influenced by the speed at which *G. aculeatus* can empty their stomach, provisioning rounds were stopped after 3 h when all individuals were satiated. A generalised linear model (GLM) was run with L_S, boldness, and sociability as fixed factors to investigate how these variables affected the total number of worms eaten. The data were fitted to a Poisson error distribution with log link function, as appropriate for count data,

and residuals were visually inspected to ensure homogeneity of variance, normality of error and linearity.

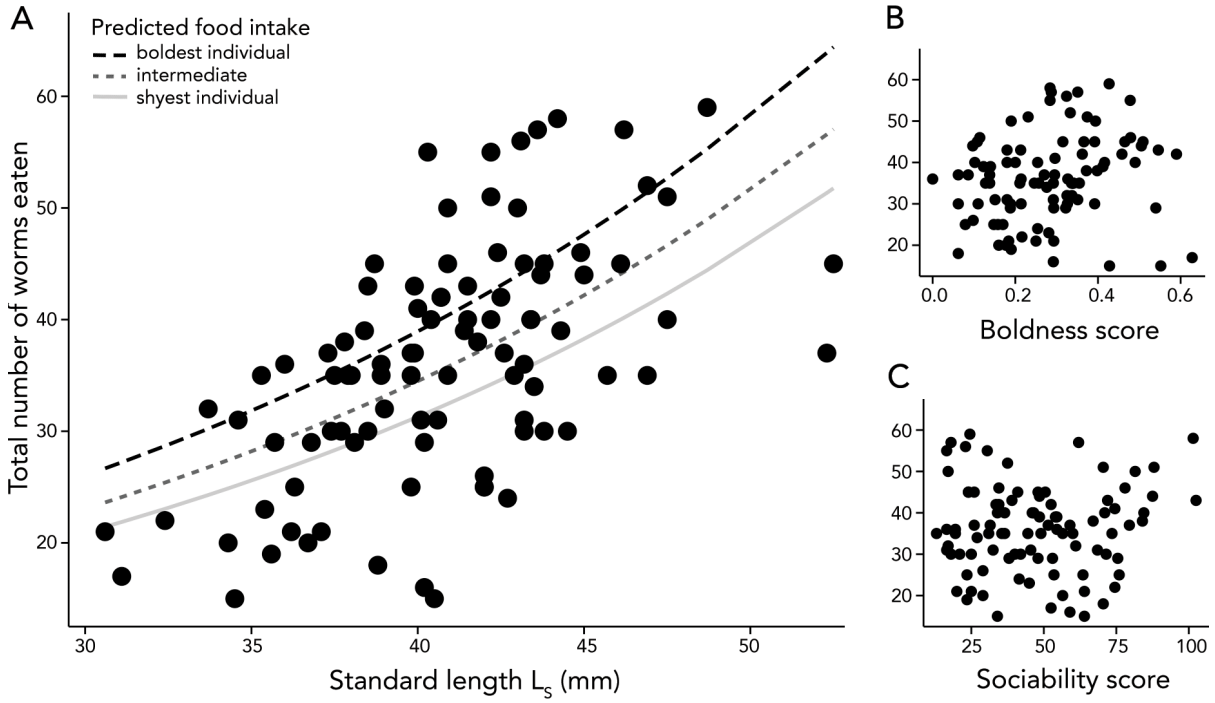

Figure 2.1. Scatterplots showing the relationship between the total number of bloodworms eaten (n = 94) and (**A**) L_S, (**B**) boldness, the average proportion of time out of cover during the risk-taking test, and (**C**) sociability, the average distance from the compartment housing conspecifics in the sociability test. Lines in plot (**A**) are predicted maximum food intake for the shyest (grey solid line), intermediate (grey dashed line), and boldest individual (black dashed line).

The maximum number of worms eaten during the feeding experiment varied considerably among individuals, ranging from 15 to 59 worms (mean ± S.E. = 36.1 ± 1.1). L_S was the strongest predictor of food intake, with larger individuals eating significantly more worms ($p < 0.001$; Table 2.1; Figure 2.1A), although relative food intake in terms of percentage body mass dropped with body mass ($r_s = -0.43$, $p < 0.001$). These findings were unsurprising as larger individuals have larger stomachs and can thus consume more food and are in line with the common finding that across teleost fishes a larger body mass is linked to a higher *overall* RMR but lower *mass-specific* RMR (Clarke & Johnston, 1999). Next to L_S, also boldness was positively correlated with maximum food intake ($p = 0.007$; Table 2.1; Figure 2.1B). Keeping L_S constant at the average L_S (40.7 mm), the shyest and boldest individuals were predicted to still vary up to 20% in their food intake (32.2 and 40.1 bloodworms respectively; Figure 2.1A). This shows that individuals with different personality types differ in their food intake even when inactive, i.e. not engaging in energetically expensive activities (Biro & Stamps, 2010) and when foraging is not directly linked to risk-reward trade-offs. This complements existing evidence that bolder individuals tend to have higher feeding rates (Biro & Stamps, 2008; Ioannou et al., 2008), but is the first time this relationship has been shown for individuals at rest.

Table 2.1 Coefficients of GLM on the maximum number of bloodworms eaten by food-deprived Gasterosteus aculeatus

	Estimate	S.E.	Wald statistic (χ^2)	*p*
L_S (mm)	0.05	0.00	93.03	< 0.001
Boldness	0.35	0.13	7.31	0.007
Sociability	0.00	0.00	0.00	0.959

Data were fitted to a Poisson distribution with log link function (*n* = 94). Backward stepwise elimination was used and statistics for non-significant terms were obtained by adding the non-significant term to the minimal model.

Various mechanisms may explain why even the food intake of sticklebacks that were inactive was positively linked to their boldness. First of all, bolder individuals may have relatively larger stomachs than shyer fish and are therefore able to eat for longer. Secondly, bolder individuals may have a stronger motivation to eat, with shyer individuals not continuing to feed to the same 'fullness' level. Thirdly, bolder individuals may be able to eat more due to a faster metabolism and/or digestion of food in their stomach, therefore enabling them to empty part of their stomach more quickly. Rapid digestion may especially be expected as the individual *G. aculeatus* had minimal stomach contents at the start of the experiment. All these explanations fit the 'performance model' (Careau et al., 2008; Careau & Garland, 2012) and pace-of-life theory (Réale et al., 2010b), which suggests an active, risky lifestyle is associated with well-developed machinery for acquiring and processing food (Biro & Stamps, 2010), supporting the idea that boldness is linked to life history strategies (Stamps, 2007; Wolf et al., 2007). These results are in line with the finding that proactive individuals had higher metabolic rates (Huntingford et al., 2010) and that individuals with higher metabolic rates show increased risk-taking behaviour after food deprivation (Killen et al., 2011), since a larger 'metabolic engine' may come with higher maintenance costs (Biro & Stamps, 2010). Bold compared to shy individuals were not simply more motivated to feed because of having a larger L_S as the two were uncorrelated in this study, in line with other work on *G. aculeatus* (Chapter 3-6; Bell & Sih, 2007). As bolder individuals are more likely to consume prey in a risky environment (Ioannou et al., 2008), and foraging fishes are less able to detect predators and predators more likely to target foraging prey (Krause & Godin, 1996), it may be suggested that risk is an important explanatory factor in the finding that bolder individuals had higher food intake. However, this possibility is not likely as food was provided on a feeding dish at the plant cover, thus enabling individuals to eat while remaining concealed under cover. Furthermore, individuals were inactive and tested in their small home compartment after 3 weeks of acclimation time. Finally, fish were given 30 min to finish a batch of bloodworms despite being able to finish it within seconds after provisioning (Jolles JW pers. obs.). Future work could examine the link between boldness repeatability and metabolism in more detail by assessing metabolite concentrations in the water of individually-housed fishes (see also Killen

et al., 2011, 2012), and investigate the possibility that shyer individuals may compensate for lower food intake by showing reduced activity.

In contrast to boldness, sociability was not linked to maximum food intake ($\chi^2 = 0.00$; $p = 0.959$; Table 2.1; Figure 2.1C). This result was predicted, since sociability is a personality trait that is not directly linked to energy production or metabolism. Nevertheless, it is likely that sociability has important indirect links to energy requirements. For example, more sociable individuals may have higher hydrodynamic benefits (Herskin & Steffensen, 1998) related to their spatial positioning in moving shoals (Chapter 5 and 6), but may also have higher energy needs due to lower potential likelihood to discover food patches as well as scramble competition. To our knowledge, this study is the first to test for an association between sociability and energetics (see Careau & Garland, 2012). Future work is required to further investigate the link between sociability and energetics (see also Réale et al., 2010), which may help to better understand the adaptive significance of sociability variation.

The results presented here on the feeding rates of food-deprived *G. aculeatus* may be helpful for future fish studies that are focused on foraging dynamics or aim to use food reward paradigms, as they show that adult fish are capable of eating up to 36 bloodworms on average, or 0.46 g bloodworms in wet mass, in a relatively short time scale (~1-3 h). Although no direct weight measurements were available, based on a large number of L_T-mass estimates of *G. aculeatus* it was calculated that individuals ate roughly 32.0% of their body mass. This is very high considering that in the wild *G. aculeatus'* average daily food intake rates have been shown to range between ~1.5% and 16.9% of their body mass (Beukema, 1968; Manzer, 1976; Rajasilta, 1980; Allen & Wootton, 1984). However, this may for a large part be explained by the high wet mass of the food, ~80% for *Chironomidae* (Armitage, Pinder & Cranston, 2012). Ultimately food intake is limited by the capacity of a well-filled stomach, predicted to equal about 5.5% body mass (Beukema, 1968), and digestion rate, up to 15% stomach contents/hour (Rajasilta, 1980). These results highlight that researchers studying personality traits and planning to use food rewards, such as for investigating the stability of personality or learning effects, should take into account that shy and bold fishes show intrinsic feeding differences irrespective of their body size.

In conclusion, individual three-spined sticklebacks at rest varied considerably in their maximum food intake, even after accounting for body size. This variability correlated positively with boldness but not with sociability, as predicted by individual differences in life-history strategies and growth-mortality trade-offs associated with these personality traits.

Chapter 3

Recent social conditions affect boldness repeatability in individual sticklebacks

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Animal Behaviour, in press

Abstract

Animal personalities are ubiquitous across the animal kingdom and have been shown both to influence individual behaviour in the social context and to be affected by it. However, little attention has been paid to possible carryover effects of social conditions on personality expression, especially when individuals are alone. Here we investigated how the recent social context affected the boldness and repeatability of three-spined sticklebacks, *Gasterosteus aculeatus*, during individual assays. We housed fish either solitarily, solitarily part of the time or socially in groups of four, and subjected them twice to a risk-taking task. The social conditions had a large effect on boldness repeatability, with fish housed solitarily before the trials showing much higher behavioural repeatability than fish housed socially, for which repeatability was not significant. Social conditions also had a temporal effect on the boldness of the fish, with only fish housed solitarily taking more risks during the first than the second trial. These results show that recent social conditions can thus affect the short-term repeatability of behaviour and obfuscate the expression of personality even in later contexts when individuals are alone. This finding highlights the need to consider social housing conditions when designing personality studies and emphasises the important link between animal personality and the social context by showing the potential role of social carryover effects.

3.1 Introduction

It is now well known that animal personalities are omnipresent in the animal kingdom (Sih et al., 2004a; Réale et al., 2007, 2010a). These consistent individual differences in behaviour play a fundamental role in the social organisation of animals (Pike et al., 2008; Croft et al., 2009; Webster & Ward, 2011; Sih et al., 2012; Aplin et al., 2013) and have considerable impact on a range of evolutionary and ecological processes (Réale et al., 2007, 2010a; Smith & Blumstein, 2008; Sih et al., 2012; Wolf & Weissing, 2012). However, while the number of studies that document the existence of animal personalities continues to grow (Réale et al., 2007; Sih et al., 2012), there is still a lack of knowledge about the stability of personality traits and the factors that may affect it (Bell & Stamps, 2004; Dingemanse et al., 2010; Laskowski & Pruitt, 2014).

The social environment is one of the major modulating factors of individual behaviour (Webster & Ward, 2011; van den Bos et al., 2013), and may both restrict and enhance individuals' behavioural responses (Webster & Ward, 2011). For example, individual fish are more active and exploratory in a social group (Gómez-Laplaza & Morgan, 1986; Webster et al., 2007; Jolles et al., 2014), but more persistent in their attention to a novel moving object when alone (Gómez-Laplaza & Morgan, 1986). Personality differences affect individual behaviour in a social context, such as their risk-taking behaviour (Chapter 4-6; Magnhagen & Bunnefeld, 2009) and leadership (Chapter 4-6; Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Kurvers et al., 2009), producer-scrounger dynamics (Dyer, Croft, Morrell, & Krause, 2009; Jolles, Ostojić, & Clayton, 2013; Kurvers et al., 2010) and the social organisation of individuals (Aplin et al., 2013; Croft et al., 2009; Pike, Samanta, Lindström, & Royle, 2008). However, the behaviour and personality of individuals is also strongly affected *by* the social context (Webster & Ward, 2011), and individuals often behave rather plastically across social contexts (van Oers et al., 2005b; Webster et al., 2007; David et al., 2011; Morand-Ferron et al., 2011). Individuals thereby modulate their behaviour based on that of others (Reebs, 2000; Webster & Ward, 2011; Herbert-Read et al., 2012), such as that related to the composition of the group (Magnhagen & Staffan, 2005) and the sex (Schuett & Dall, 2009; Piyapong et al., 2010) and personality (Chapter 4; Magnhagen & Bunnefeld, 2009; van Oers et al., 2005) of their group mates. For example, although in three-spined sticklebacks, *Gasterosteus aculeatus*, risk-taking behaviour and leadership of individuals in a social context are positively linked to their propensity to take risks when alone ('boldness'), this effect can be strongly enhanced or reduced by the personality of their current (Chapter 4; Harcourt et al., 2009) and previous group mates (Chapter 4). Consequently, in a social group, the behavioural variance among individuals tends to be reduced (Gómez-Laplaza & Morgan, 1986; Magnhagen & Bunnefeld, 2009; Herbert-Read et al., 2012) and the personalities of individuals, quantified in individual assays, only expressed to a certain extent (Webster et al., 2007; Magnhagen & Bunnefeld, 2009; Castanheira et al., 2013). However, in relatively stable social environments, individuals are more likely to repeat certain behaviours by positive feedback from experience and optimal behaviour via repeated

interactions (Harcourt et al., 2009; Nakayama et al., 2013; Laskowski & Pruitt, 2014). These interactions may increase the behavioural variability among group members (Laskowski & Pruitt, 2014), and the behavioural repeatability of individuals (Wolf et al., 2011; Laskowski & Bell, 2013).

If the effect of the social context is so strong, could it be that it still affects the subsequent expression of personality (and thus its repeatability) when individuals are alone? This carryover effect may be likely, as the prior social context has already been shown to affect behaviour in later social contexts in terms of an individual's shoaling decisions (Chapter 4; Gómez-Laplaza, 2009), risk-taking behaviour (Chapter 4; Frost, Winrow-Giffen, Ashley, & Sneddon, 2007) and leadership (Chapter 4). Furthermore, it takes time for individuals to adjust between (social) environments, resulting in habituation (decline in behaviour) and/or acclimatization (change in behaviour) responses (Budaev, 1997; Gómez-Laplaza & Morgan, 2000; Martin & Réale, 2008; Biro, 2012), such as individuals becoming less active over solitary test trials (Martin & Réale, 2008) and showing more stable behavioural patterns after longer social isolation (Biro, 2012). Behavioural repeatability may be further compromised at the group level by the large variability in the way individuals are affected by prior social experiences (Chapter 4), and the speed (Rodríguez-Prieto, Martín & Fernández-Juricic, 2011) and extent to which they adjust to environmental change (Dingemanse & Wolf, 2013). For example, shy individuals are less affected by previous social experiences than bold individuals (Chapter 4), and show higher behavioural plasticity between social contexts in three-spined sticklebacks, perch, *Esox lucius*, and zebra finches, *Taeniopygia guttata* (Chapter 4; Magnhagen & Bunnefeld, 2009; Magnhagen & Staffan, 2005; Schuett & Dall, 2009; Webster et al., 2007).

Here we investigated to what extent recent social conditions affect the boldness and repeatability of individual three-spined sticklebacks that were either solitarily housed, solitarily housed part of the time or socially housed in small groups of four prior to two trials of a boldness test (see Table 3.1). As only fish in the solitary treatment were given time to habituate and acclimatise to being alone, we hypothesised that these fish would show the most risk-taking behaviour due to lower stress of isolation. We also hypothesised that solitary fish would show the highest repeatability in their behaviour as they had more time for social modulation effects to fade and individual variability in acclimatization responses to stabilise. Fish that were housed solitarily only part of the time were predicted to show intermediate levels of repeatability. We assessed behavioural repeatability by three of the most used indices to get a full picture of personality expression following Bell et al. (2009): agreement repeatability, the extent to which individual differences in trait scores are maintained over time relative to the change of the group (Biro & Stamps, 2015), consistency repeatability, which measures the agreement in relative measurements between individuals (Nakagawa & Schielzeth, 2010), and raw rank order consistency. The three-spined stickleback is an excellent model system to investigate these questions on personality and social dynamics (see e.g. Bell &

Stamps, 2004; Ward et al., 2005; Webster et al., 2007; Webster, Ward & Hart, 2009; Bell & Sih, 2007; Pike et al., 2008; Harcourt et al., 2009; Laskowski & Bell, 2014), as it is a social species, with a strong tendency to shoal most of the year (Huntingford & Coyle, 2010; Ostlund-Nilsson et al., 2010), but is also physically and behaviourally robust thus can be kept both solitarily and in groups in a laboratory environment (Huntingford & Ruiz-Gomez, 2009).

3.2 Methods

Subjects and housing

We collected three-spined sticklebacks using a sweep net from a tributary of the river Cam near Cambridge, UK, and housed them in an environmentally controlled laboratory for more than 4 months before the start of experiments. Ambient temperature was maintained at 14 °C and the photoperiod at 12:12 h light:dark. Fish were kept socially (ca. 200 fish) in a large glass holding aquarium (120 cm length × 60 cm width × 60 cm height) with artificial plants, aeration, and under-gravel filtration, and fed frozen bloodworms (*Chironomidae* larvae) *ad libitum* once daily. During the experimental period, fish were housed in custom holding tanks (60 cm × 30 cm × 40 cm) lined with gravel and divided lengthwise into six compartments (30 cm × 12 cm; 15 cm depth) by opaque acrylic partitions. Of each tank, five compartments were used to house fish and contained an artificial plant; the remaining compartment contained an under-gravel filter. The partitions prevented fish from seeing conspecifics in adjacent compartments and minimised the transfer of olfactory cues. All fish were of similar length (41 mm ± 0.7 mm) and age (ca. 12 months) and were taken from a single population to minimise population-specific effects that may influence personality (Bell, 2005). The temperature and photoperiod regime in the laboratory resemble early spring/late autumn conditions, and prevented the fish from coming into breeding condition (Borg, Bornestaf & Hellqvist, 2004; Ostlund-Nilsson et al., 2010). Therefore the sex of the fish could not be determined. Fish had not been used in any previous experiments.

Boldness test

To investigate an individual's propensity to take risks ('boldness'), we subjected them individually to one of eight identical white acrylic tanks (70 cm length × 15 cm width × 30 cm height) that contained gravel sloping from a deep area (14 cm depth) to an increasingly shallow 'exposed' area (4 cm depth at the other side). The deep area was covered by semitransparent green acrylic that protruded 10 cm from the back of the tank to provide shelter ('cover'). We defined fish to be out of cover only when they had emerged with their full body. Our set-up reflects the ecologically relevant situation in which a fish can either rest in a safe place or explore a risky area (in search of potential food). Fish prefer to spend time under cover but,

even in the absence of food, keep making regular trips out of cover to explore the exposed area (see also Chapter 4 and 5; Harcourt et al., 2009; Nakayama et al., 2013). To minimise any potential disturbances from outside the tanks, testing was conducted inside a white photo tent. The daily test order and assignment to test tanks was randomised. HD video cameras (Camileo X100, Toshiba Corporation, Japan) fixed above each tank were used to record the fish.

Table 3.1 Overview of the experimental schedule for the three different treatment groups.

Treatment	Day 1	Day 2	Day 3	Day 4	Day 5		Day 6	
Solitary	in group	in group	solitary	solitary	Session 1	solitary	Session 2	end
Partial solitary	in group	in group	in group	in group		solitary		end
Social	in group	in group	in group	in group		in group		end

Experimental procedure

We randomly selected 156 fish from the holding tank and housed them in groups of four in the custom housing compartments. On day 1 we randomly selected one fish from each compartment (n = 39 focal fish) and, for visual identification, attached a small coloured plastic tag on the second dorsal spine of each fish (see Webster & Laland 2009). To control for habituation and acclimatization effects (Gómez-Laplaza & Morgan, 2000; Biro, 2012), we allowed fish to acclimatise in their holding compartment for two full days. Focal fish were randomly allocated to one of three treatments and tested in the boldness test on the following two days (session 1 and 2) for one hour per day (c.f. Chapter 4; Harcourt et al., 2009). Treatment groups (n = 13 each) differed in their social conditions prior to the two boldness trials (see Table 3.1): fish were housed either (1) individually for 48 h before trial 1 as well as during the ca. 24 h period between the two trials ('solitary'), (2) socially (i.e. with the same 3 fish as before) up until the first trial but individually in the ca. 24 h period between the two trials ('partial solitary'), or (3) socially throughout ('social'). To control for the disturbance of removing the group mates from the compartments of the solitarily house fish, we used a fishnet to unsettle the water in the compartments of the other two treatment groups for 10 s. Animal care and experimental procedures were approved by the Animal Users Management Committee of the University of Cambridge as a non-regulated procedures regime.

Data analysis

Videos were tracked using custom-written tracking software using Python 2.7 and the Open CV library, checked for any tracking errors and, if needed, manually corrected. From the tracking data we determined risk-taking behaviour as the proportion of time fish were out of cover and calculated its repeatability across the two trials. To properly determine the repeatability of risk-taking behaviour we computed three measures: (1) 'agreement repeatability', a measure of change in individual's trait expression across time *relative* to the

change of the group (Lessells & Boag, 1987), using Analyses of Variance; (2) 'consistency repeatability', which measures the agreement in *relative* measurements between individuals (Nakagawa & Schielzeth, 2010), using Analyses of Variance with normalised data; and (3) rank order consistency, using robust Spearman rank correlation tests. Significance of repeatability was calculated by running 10 000 permutations of each test. To investigate temporal changes in risk-taking behaviour we fitted linear mixed models with proportion of time out of cover as the response variable, trial, treatment group and the interaction between them as fixed factors, and fish ID as a random factor. Minimal adequate models were obtained by comparing models based on log likelihood using backwards-stepwise elimination, starting with the full model. Residuals were visually inspected to ensure homogeneity of variance, normality of error and linearity. We used paired *t*-tests to investigate whether risk-taking behaviour differed between the two trials separately for each treatment group. Body size was not correlated with boldness ($p > 0.1$), in line with previous stickleback work (Chapter 5; Bell & Sih, 2007; Webster, Ward, & Hart, 2009), and was not fitted as an additional predictor in the models. All results with $0.1 > p > 0.05$ are reported as trends and $p < 0.05$ as significant. Means are quoted ± SE throughout. All data were analysed in R 3.0.2.

3.3 Results

On average, individuals spent 37.7% of their time out of cover. However, there was considerable inter-individual variation, with some individuals only spending 3.5% of their time out of cover and others up to 62.6% during a session (Figure 3.1). Overall, this individual variability in boldness was significantly repeatable across the two trials, in terms of raw consistency, consistency repeatability and agreement repeatability (Table 3.2).

Table 3.2 Rank order consistency, consistency repeatability and agreement repeatability of the proportion of time individuals spent out of cover ('risk-taking') across the two trials of the boldness test, for each of the three treatment groups (n = 13 each) separately and for all fish overall.

	Rank order consistency	Consistency repeatability	Agreement repeatability
Solitary	0.61 [0.10, 0.87] p = 0.026	0.64 [0.27, 1.0] p = 0.007	0.38 [-0.14, 0.91] p = 0.081
Partial solitary	0.50 [-0.07, 0.83] p = 0.073	0.53 [0.09, 0.98] p = 0.023	0.51 [0.05, 0.96] p = 0.030
Social	0.06 [-0.50, 0.60] p = 0.823	0.11 [-0.50, 0.72] p = 0.348	0.13 [-0.47, 0.74] p = 0.321
Overall effect	0.37 [0.06, 0.61] p = 0.020	0.38 [0.10, 0.66] p = 0.007	0.38 [0.10, 0.66] p = 0.008

95% confidence intervals are given in brackets.

If the social context continues to affect individual variability in behaviour even when fish are alone, then the behaviour of solitarily housed individuals should be more repeatable than that of individuals housed in a group. We found support for this hypothesis as fish housed solitarily were the only group to show significant rank order consistency and had the

highest consistency repeatability, based on Analyses of Variance with normalised data to control for time effects (Table 3.2). However, in terms of agreement repeatability, there was only a non-significant trend for solitarily housed fish to show repeatability, while the behaviour of fish housed solitarily only the day before the second trial was repeatable. As for the other measures, fish housed socially did not show repeatability (Table 3.2).

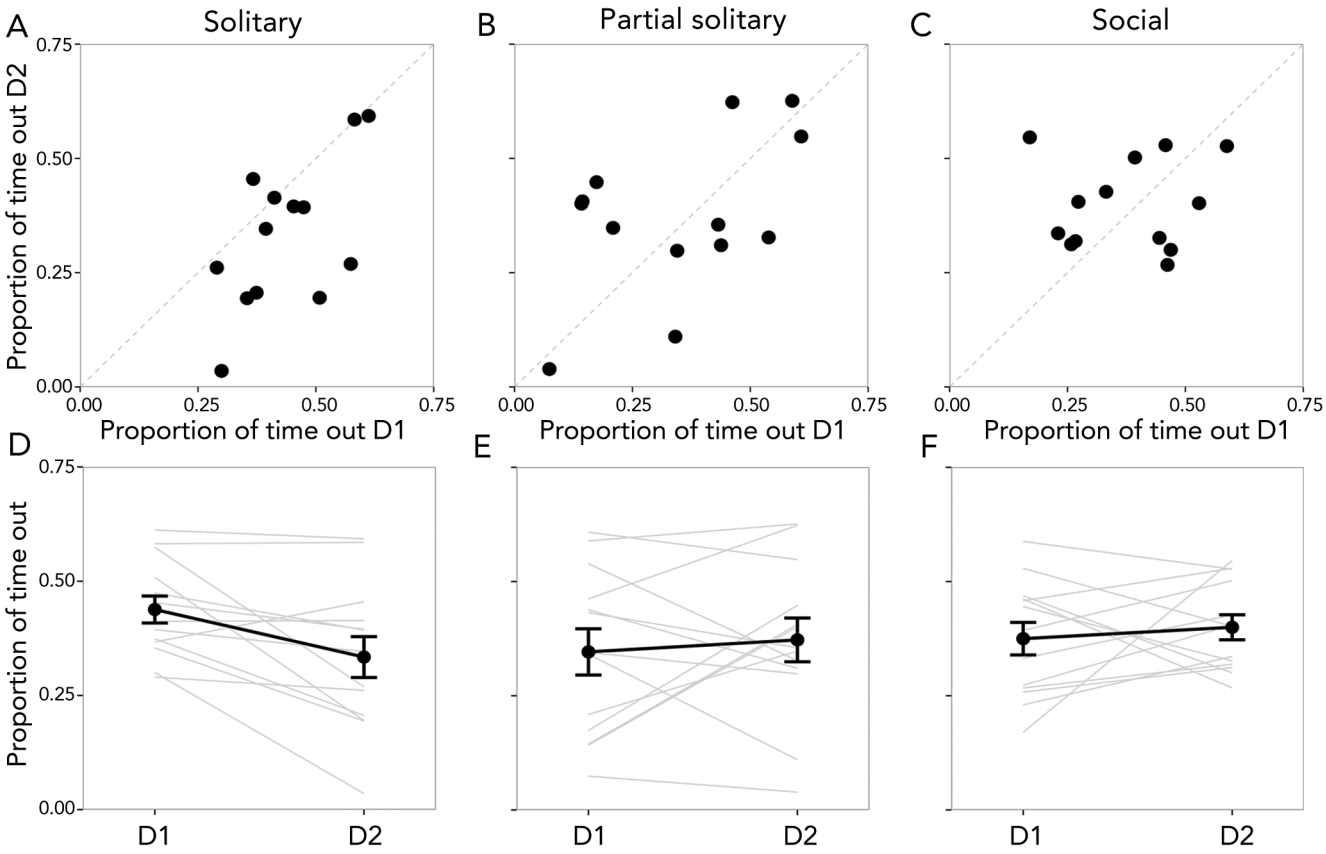

Figure 3.2 Plots showing the proportion of time that fish were out of cover during the first trial (D1) and the second trial (D2), highlighting the difference in boldness expression (proportion of time out of cover) for fish that were (**A** and **D**) housed solitarily, (**B** and **E**) housed socially until the first test trial but solitarily until the second trial (partial solitary), or (**C** and **F**) housed socially throughout. Both scatterplots (**A**, **B**, **C**) and line plots (**D**, **E**, **F**) are presented to illustrate differences in rank order consistency, repeatability and temporal changes in risk-taking behaviour. In the line plots, grey lines depict individual responses, black lines depict group average responses and vertical black bars depict standard errors.

Table 3.3 Analyses of mean level change and variance across the two trials of the boldness test for each of the three treatment groups separately (n = 13 each) and for all fish overall.

	Mean level change			Equal variance		
Solitary	t_{12} = 2.94	p = 0.012	Yes	$F_{12,12}$ = 0.43	p = 0.162	Yes
Partial solitary	t_{12} = -0.54	p = 0.602	No	$F_{12,12}$ = 1.11	p = 0.854	Yes
Social	t_{12} = -0.57	p = 0.577	No	$F_{12,12}$ = 1.70	p = 0.372	Yes
Overall effect	t_{38} = 0.67	p = 0.504	No	$F_{38,38}$ = 0.97	p = 0.923	Yes

Besides the differences in repeatability, the social context also affected the mean time individuals spent out of cover across both days (trial*treatment group interaction: $\chi^2 = 6.85$, $p = 0.033$): while fish housed solitarily spent significantly more time out of cover during the first than the second trial, fish from the partial social and social treatment groups did not change their behaviour significantly between trials (Figure 3.1, Table 3.3). The three treatment groups did not differ in the total time spent out of cover in the test after pooling the data of both trials ($F_{2,36} = 0.22$, $p = 0.805$). There was no significant difference in the variance in time spent out of cover between days for all treatment groups (Table 3.3).

3.4 Discussion

By keeping fish either solitarily or in a small group and subjecting them to repeated individual boldness assays, we aimed to uncover how personality expression in an individual context may be affected by prior social conditions. Although overall the behaviour of the fish was repeatable, that of fish that were housed solitarily before the personality trials was much more repeatable than that of fish housed socially, for which repeatability was not significant. Furthermore, social conditions experienced before the individual trials also affected the mean level change in boldness over time, with solitarily housed fish being bolder during the first than the second trial.

The finding that the behaviour of fish housed solitarily before the individual trials was repeatable while that of socially housed fish was not, as indicated by both rank order consistency and consistency repeatability, may potentially be explained by modulating effects of the social environment (Webster & Ward, 2011; van den Bos et al., 2013). Previous work that compared fish in isolation versus in a group context showed that individuals take more risks (Chapter 4; Magnhagen & Bunnefeld, 2009), are more active (Gómez-Laplaza & Morgan, 1991; Webster et al., 2007) and show less attention to a moving novel object (Gómez-Laplaza & Morgan, 1986) when kept in a group, but that behavioural variability among individuals is generally higher when individuals are kept solitarily (Gómez-Laplaza & Morgan, 1986; Magnhagen & Bunnefeld, 2009). Despite being tested alone, social effects are likely to carry over to the individual test trials and compromise individual's personality expression due to the recency of the social context but the effect would be much less for fish in the solitary treatment group as they had already been isolated for two days. Such effects may be likely, as social experiences have been shown to carry over from one social context to the next (Chapter 4; Frost et al., 2007; Gómez-Laplaza, 2009), and also after a few days of exposure to the social context, as sticklebacks may already prefer familiar individuals after 24 h (Ward et al., 2005). A second factor that is likely to have caused at least part of the difference in repeatability between the treatment groups is the effect of habituation and/or acclimatisation (Wilson et al., 1993; Bell & Peeke, 2012; Biro, 2012). Only solitarily housed fish had time to acclimatise to being alone, as

they would be when in the boldness environment, and individual variability in the way animals respond to changes in their environment may have compromised the behavioural repeatability of the socially housed treatment group. That is, individuals often have unique individual-specific patterns of acclimatization and habituation (Bell & Peeke, 2012; Biro, 2012). Furthermore, individuals with different personalities often have different rates of habituation, for example more easily trapped fish in the wild habituate sooner to social isolation in the laboratory (Wilson et al., 1993), and different levels of social responsiveness (Chapter 5) and plasticity of behaviour, for example shyer individuals adapt more readily to their current social environment (Chapter 4; Magnhagen & Bunnefeld, 2009). It may be hypothesised that fish experienced the removal of conspecifics as a predation threat. However, this is unlikely since the risk-taking behaviour of solitary fish was higher and not lower, as would be expected, and that of fish within the social-asocial treatment group did not decrease in the second trial. As the fish in our study had relatively short exposure to their social context, approximating the relatively fluid, high-turnover groups of sticklebacks in the wild (Croft et al., 2005; Ward et al., 2002), the positive effect of social isolation on the repeatability of behaviour is most likely to be the result of the recent social context obfuscating personality expression rather than determining it. However, long-term exposure to a stable social environment may actually increase behavioural repeatability (Wolf et al., 2011; Laskowski & Pruitt, 2014). For example, a study on male water striders showed that the behaviour of individuals housed socially throughout their lives was repeatable while that of non-socially housed individuals was not (Han & Brooks, 2014). Such effects are probably species dependent, relative to the stability of the social environment, and longer social exposure may not generate personalities in sticklebacks (Laskowski & Bell, 2014). An exciting area for future research would be to investigate how the behavioural repeatability and personality expression of adult individuals may still be affected by or even accounted for by social experiences early in life.

It is important to note that, had we used agreement repeatability as our personality index, we would have reached slightly different, less valid conclusions based on the low repeatability and low significance of this measure (Table 3.2). Despite being one of the most popular personality indices, it is often overlooked that agreement repeatability ignores any time-related change (Biro & Stamps, 2015). That is, this index looks at the change in an individual's trait expression across time relative to the change of the group (Nakagawa & Schielzeth, 2010). Although in our study the variance among individuals was the same in both trials for all treatment groups (see Table 3.3), complying with the first assumption of repeatability analyses (Bell et al., 2009), the significant drop in mean boldness of the solitarily housed fish would result in biased and invalid repeatability estimates. We corrected for such mean level changes by normalising the behaviour for each group and trial, and found that, relatively, the inter-individual variability in risk-taking behaviour was the most repeatable for the solitary fish. This was further confirmed by Spearman rank correlations. These analyses

together highlight that it is important to consider the potential of mean level changes in behaviour in one's data, an aspect that is often ignored in personality studies (Bell et al., 2009; Biro & Stamps, 2015) beyond those that specifically focus on it (see Dingemanse et al., 2010; Dingemanse & Wolf, 2013).

The social conditions prior to the individual trials also had a temporal effect on the boldness of the fish: solitarily housed fish spent significantly more time out of cover during the first than the second trial, while no such effect was found for fish housed socially. The temporal difference in boldness between the groups is probably related to the acclimatisation time to isolation (Biro, 2012). The change from the housing compartment to the solitary boldness environment was much less for fish housed solitarily already than for those housed socially until the start of the personality trial, which may have resulted in an increase in stress from social separation (see Gallup & Suarez, 1980). As a result, these fish may have been less willing leave cover and explore the novel open environment. Previous research has suggested that isolated individuals may be more active because of their motivation to seek conspecifics, especially after recent social separation (Gallup & Suarez, 1980; Gómez-Laplaza & Morgan, 1991). However, it is unlikely that the observed higher activity of solitary housed fish reflects social reinstatement behaviour. That is, in contrast to our study, these studies did not provide cover in their test environment, so individuals might have best reduced their predation risk by seeking others and staying close to them (Pitcher & Parrish, 1993). Other studies that used the same test set-up have shown that boldness in this task is strongly positively linked to foraging, risk-taking behaviour and leadership in a group context (Ioannou et al., 2008; Harcourt et al., 2009; Nakayama et al., 2013), highlighting that the behaviour observed during the individual test trials does not reflect social motivation. Although no robust measures of behavioural reaction norms could be acquired in the present study (see van de Pol, 2012), visual inspection of the temporal change in behaviour (Figure 3.1D-F) shows considerable inter-individual variation, especially in the way individuals responded to the social-asocial switch (partial social treatment; Fig. 1E). An exciting avenue for future research would be to investigate behavioural reaction norms and plasticity in the way animals adapt between social and solitary environments.

Given the lack of agreement in the literature about how we should sample, design experiments and assay personality traits, it is important to evaluate our approaches and definitions (Carter et al., 2013; Biro, 2013). This study contributes to this process by showing that social (housing) conditions may affect the short-term stability of personality expression and that social isolation may improve its repeatability. Our results thus highlight that it may often be advisable to isolate individuals for a number of days prior to testing so as not to obfuscate personality expression during individual assays. However, care should be taken as many social species do not deal well with complete isolation, and long-term effects of social isolation, such as over a lifetime, may be detrimental to the repeatability of individual

behaviour (Han & Brooks, 2014). Therefore the best option may be to separate individuals while allowing (some) visual and/or auditory cues of conspecifics, depending on the study system. Such result-based suggestions may be particularly relevant as studies vary considerably in the social conditions prior to individual testing, with many studies removing individuals from their social environment, either directly from the field or from their social laboratory housing (see Biro, 2012), and subsequently observe their responses during individual behavioural assays (see Webster & Ward, 2011). It is also relevant, in the context of the present study, to highlight that personality studies vary considerably in the number of times individuals are assayed. Most studies, including ours, test individuals only twice, which is generally sufficient when one is only concerned with linking a specific personality trait with another variable of interest. However, considerably more observations per animal and/or larger sample sizes may be required to get more accurate and robust repeatability estimates (Dingemanse & Dochtermann, 2013; Biro & Stamps, 2015), to rigorously characterise individual behavioural types (Biro, 2012; Biro & Stamps, 2015), and to investigate between-individual variability in plasticity and behavioural reaction norms (Dingemanse et al., 2010; Dingemanse & Wolf, 2013). An increasing number of studies actually assay individuals only once, implicitly assuming that behavioural traits are highly consistent over time (Garamszegi, Markó & Herczeg, 2012; Beckmann & Biro, 2013). Our findings highlight that such individual assays in personality research could lead to highly biased measures (c.f. Beckmann & Biro, 2013; Biro & Stamps, 2015; Biro, 2012), especially when social conditions prior to testing are not considered.

To conclude, we have shown that social isolation prior to individual personality assays can improve the short-term repeatability of behaviour as recent social experiences may obfuscate personality expression. Our study adds to the increasing literature that investigates the link between animal personality and the social context (Webster & Ward, 2011), but is conceptually different from the majority of studies that have only considered social modulation effects in the social context itself. Our findings have important practical consequences for the design of personality assays, as they highlights that it is critical to consider the social conditions before such assays. Furthermore, they contribute to our understanding of the link between animal personality and the social context by emphasising the role of carryover effects of social experiences on the stability of personality expression.

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Chapter 4

The role of previous social experience on risk-taking and leadership in three-spined sticklebacks

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Abstract

The emergence of leaders and followers is a key factor in facilitating group cohesion in animals. Individual group members have been shown to respond strongly to each other's behaviour and thereby affect the emergence and maintenance of these social roles. However, it is not known to what extent previous social experience might still affect individual's leading and following tendencies in later social interactions. Here, by pairing three-spined sticklebacks (*Gasterosteus aculeatus*) with two different consecutive partners, we show a carry-over effect of a previous partner's personality on the behaviour of focal individuals when paired with a new partner. This carry-over effect depended on the relative boldness of the focal individual. Relatively bold but not shy fish spent less time out of cover and led their current partner less if they had previously been paired with a bolder partner. By contrast, following behaviour was mainly influenced by the personality of the current partner. Overall, the behaviour of relatively bold fish was more consistent across the stages while shy fish changed their behaviour more strongly depending on the current context. These findings emphasise how the history of previous social interactions can play a role in the emergence and maintenance of social roles within groups, providing an additional route for individual differences to affect collective behaviour.

4.1 Introduction

The emergence of leaders and followers plays a major role in promoting group coordination and cohesion, with important consequences for the social lives of humans as well as many non-human animals (Krause & Ruxton, 2002; Conradt & Roper, 2009; Dyer et al., 2009b; King et al., 2009). There is a growing body of evidence that individuals differ in their social roles, with some individuals having a strong influence on group behaviour while others mostly follow (e.g. Reebs 2000; Harcourt et al. 2009; Nagy et al. 2010; Flack et al. 2012; Nakayama et al. 2013). A key focus has been to determine what factors predict which group members will become leaders (Conradt & Roper, 2003; Couzin et al., 2005; King et al., 2009). Many such factors have been identified in a large range of species: body size (Krause et al., 1998; Reebs, 2001), hunger level (Krause et al., 1998; McClure, Ralph & Despland, 2011; Nakayama et al., 2012b), dominance (Peterson & Jacobs, 2002; King et al., 2008; Jolles et al., 2013a), social affiliations (King et al., 2008; Jacobs et al., 2011), sex (Peterson & Jacobs, 2002; Barelli et al., 2008), age (Réale & Festa-Bianchet, 2003; Sueur & Petit, 2008), boldness (Beauchamp, 2000; Ward et al., 2004; Harcourt et al., 2009; Kurvers et al., 2009), sociability (Brown & Irving, 2014), and knowledge or experience (Reebs, 2000; Couzin et al., 2005; Dyer et al., 2009b; Flack et al., 2012).

In recent years a few studies have started to go beyond the search for such predictive factors and have shown that the actual dynamics of interactions amongst individuals play an important role in leading and following behaviour (Harcourt et al., 2009; Nakayama et al., 2012a, 2013; Ward et al., 2013; Pettit et al., 2013). For example, although bold individuals typically lead and shy individuals mainly follow (Beauchamp, 2000; Harcourt et al., 2009; Kurvers et al., 2009; Nakayama et al., 2013), these differences in leading and following are strongly enhanced by social feedback (Harcourt et al., 2009; Nakayama et al., 2012a). Furthermore, although bolder individuals are generally less responsive to their partner's behaviour, both bolder and shyer individuals readily adjust to their partner when in the following role (Nakayama et al., 2012a,b). These findings not only highlight the important modifying role of social feedback, they also suggest the exciting possibility that interactions with previous partners may play a role in later leading and following behaviour. As also highlighted in the human leadership literature (Amit et al., 2009; Emery, 2010; DuBrin, 2013), addressing this key outstanding issue may contribute to our understanding of the emergence and maintenance of leadership and ultimately of collective behaviour and group decision-making.

Most gregarious animals live in highly dynamic groups in which they interact with multiple conspecifics (Krause & Ruxton, 2002), and a strong influence of previous social experience has already been shown for neophobic and aggressive behaviour (Hsu & Wolf, 1999; Frost et al., 2007). In a previous study on leadership, three-spined sticklebacks were found to change their behaviour based on a partner's ability to successfully locate food during joint trips, with experience overriding personality differences in follow but not leading

tendencies (Nakayama et al., 2013). Here by pairing three-spined sticklebacks (*Gasterosteus aculeatus*) with two different consecutive partners, we investigated how previous social experience with other individuals affected the propensity of fish to leave cover, to lead, and to follow their current partner during joint trips. If individuals fine-tune their behaviour based on previous experiences this potentially represents a mechanism through which social roles can be reinforced. Since bold individuals are known to be less responsive than shy individuals during social interactions (Pike et al., 2008; Nakayama et al., 2012a,b), we hypothesised that bolder fish would be more consistent in their behaviour across different social and non-social environments, and shyer fish to be more responsive to the present context. We therefore predicted that the behaviour of bolder fish would be mainly explained by their own personality and to a lesser extent by that of their current and previous partners, while for shyer fish the personality of their current partner would be the main determinant of their behaviour. This approach provides a unique opportunity to describe important new aspects of social feedback and personality that have thus far been neglected in studies on group movements and leadership.

4.2 Methods

Subjects and housing

We collected three-spined sticklebacks using a sweep net during the summers of 2010 to 2012, from a small branch of the river Cam (Cambridge, UK). Large groups of fish (~ 200 individuals) were housed in a temperature-controlled laboratory (T = 14°C ± 1°C) with a constant light regime (lights on from 09:00 to 19:00 h) and kept in large glass holding aquaria (120 cm width x 60 cm length x 60 cm height) that contained artificial plants, aeration and under-gravel filtration. Fish were fed frozen bloodworm (*Chironomidae* larvae) *ad libitum* once a day before the start of the experiment. During the experimental period, feeding was rationed to one bloodworm a day. All fish used for the experiment were of similar length (50 mm ± 7 mm from tip of snout to caudal peduncle) and were taken from a single population to minimise population-specific genetic effects that may influence personality (Bell, 2005). Although the exact age of the fish could not be determined, all caught individuals were juveniles and are expected to only vary in age by a few weeks. Sex of the fish was not identified as the temperature and photoperiod regime in the lab prevented the fish from becoming sexually mature (Borg et al., 2004).

Experimental set-up

During the experimental period we housed fish individually in custom holding tanks (60 cm x 30 cm x 40 cm) lined with gravel and divided lengthwise into six compartments by transparent

Perspex partitions. Five compartments were used to house a fish each and contained an artificial plant at one end and a white Perspex plate (2 x 2 cm) at the other end where food was delivered. The remaining compartment contained the under-gravel filter and was not used to house any fish. Partner fish were never housed in adjacent compartments. Fish were allowed to acclimatise in their individual compartments for three days before the start of testing.

To investigate fish's propensity to explore a risky area and lead and follow conspecifics, we used a tank set-up previously used in our lab for similar experiments (Harcourt et al., 2009; Nakayama et al., 2012a,b). In short, experiments took place in four identical experimental tanks (70 cm x 30 cm x 30 cm), each divided lengthwise with either an opaque white Perspex partition or a transparent Perspex partition to create two long lanes (see Figure 4.1). Each lane was lined with gravel in a slope ranging from a deep (15 x 15 cm; 14 cm depth) 'safe area' that contained an artificial plant to an increasingly shallow 'exposed' area (4 cm depth at the other side). Only when fish had fully emerged from this safe area we defined them to be 'out of cover'. No food was provided during the trials and fish were thus not rewarded for leaving cover. This set-up reflects the ecologically relevant problem where fish can either rest in a safe place or explore a risky area in search of food (analogous to the exposed area where food is delivered in their holding compartments). Fish prefer to spend time under cover but, even in the absence of food in the experimental tank, keep making regular trips out of cover to explore the exposed area. Since fish have different preferences for the number and length of trips out of cover they make, yet prefer to synchronise their activities and shoal together, there is a conflict on the timing of leaving and returning to cover. We have used this ecologically relevant setup to look at the emergence of leaders and followers in a number of previous papers (e.g. Harcourt et al. 2009, 2010). The walls of the tank were covered by white Perspex to minimise any disturbances from outside the tank. When not running experiments, the water of the experimental tanks was oxygenated with an air stone. HD video cameras (Camileo X100, Toshiba Corporation, Japan) were used to record fish movements from a fixed position above each tank.

Experimental procedure

We tested four batches of fish (n = 136 in total), each over a 7-day cycle (Nov-Dec 2011 and Nov-Dec 2012) and randomly selected 44 fish as focals, 44 as partner for the 'first pairing', and 44 as partner for the 'second pairing'. Fish were tested across three stages. We started by testing fish in the experimental tank in isolation to quantify their boldness ('isolation stage'). On day one and two, each fish was put in one of two lanes of the experimental tank that were separated by an opaque partition so that fish could not interact with each other. The behaviour of each fish was recorded for an hour each day. After a rest day, we randomly paired each focal fish with a partner ('previous pairing stage'), and put the two fish in the same experimental tank, but this time with a transparent partition so that they could interact. Behaviour was

recorded for an hour on each of two consecutive days. Finally, we paired each focal with a new socially naïve partner and observed their behaviour for another two one-hour sessions over two consecutive days ('current pairing stage'). The only difference between the two pairings was the identity of the partner. On each testing day, fish were transferred to the deep end of the tank using a dip net and allowed to acclimatise to the tanks for seven minutes before we tracked their movements. After each trial, fish were moved back to their housing compartment. For each experimental cycle, we randomised the daily testing order as well as the assignment to tank and to the left and right lanes of a tank. Fish were housed in their individual compartments for a week before their first pairing to minimise any social experiences from being housed with conspecifics in social housing tanks.

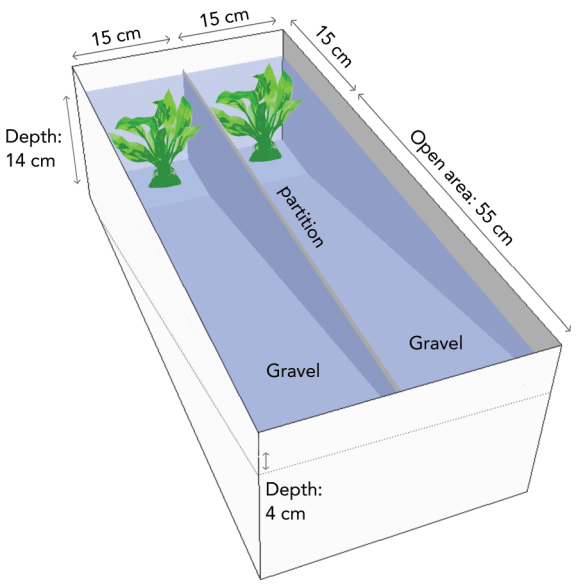

Figure 4.1 Schematic overview of the experimental set-up consisting of two lanes separated by either an opaque or transparent partition containing a safe deep area (15 cm length) and a shallow open 'risky' area (55 cm length).

Data analysis

We tracked the exact movements of the fish at 10 frames/s using automated motion tracking software (AnTracks, version 0.99). For tracking we used a background subtraction acquisition method that determined what pixels differed between the video and a background image that was created from a random five-minute period in each one-hour recording. As processing parameters we used gauss subtraction, gauss blur, dilate and final tresholding for which we adjusted the levels according to the specific light levels in each video to ensure fish movements were tracked correctly. After tracking was complete we checked all trajectories for each video. Any possible noise tracked by the software was eliminated and discontinuous trips where the software had lost track of the fish for a few frames were joined.

Data were analysed in R 3.0.2 (R Development Core Team). Based on the positional coordinates of both members in a pair we calculated the relative time fish spent out of cover

and their number of trips out of cover. On average, fish spent 12.89 % of the time out of over (range 0 - 62.3 %) and were consistent in this proportion of time out of cover across the two days of the isolation stage (r_s = 0.55, n = 136, p < 0.001). Therefore we used the average proportion of time individuals were out of cover across both days as the boldness score for each fish, an approach commonly adopted for examining the boldness personality trait (e.g. Harcourt et al., 2009; Magnhagen & Bunnefeld, 2009; King et al., 2013). Ten fish that did not come out of cover during the isolation stage were excluded.

The behaviour of pairs of fish in a similar setup but without previous experience has been described in detailed in previous work (Harcourt et al., 2009; Nakayama et al., 2012a,b, 2013). In this paper, we focus on the effect of previous experience (the first pairing) on later interactions (the second paring). We focused on the proportion of time spent out of cover by the focal fish, and on the number of trips it made out of cover on its own, as a leader, and as a follower. Leading was defined as a fish going out of cover and being joined by its partner; following as a fish going out of cover to join its partner that is already out. We considered the effects on leading and following behaviour separately as previous work has shown that different factors (e.g. success of a partner in finding food) may affect the tendencies to lead and follow in different ways (e.g. Nakayama et al., 2013). For each of the four variables (time out of cover, and the three types of trips), we used linear models with the focal fish own boldness, the boldness of the previous partner and that of the current partner as predictors. We started with full models with all the predictors, and obtained a minimal model by backwards-stepwise elimination (i.e. sequentially dropping terms until all terms retained in the model were significant). Statistics for non-significant terms were obtained by fitting the minimal model with each non-significant term added individually. As previous work has shown that the relative personality between partners is a key predictor of collective movements and leadership (Harcourt et al., 2009; Nakayama et al., 2013), we ran separate models for focals bolder than their second partner (bold focals) and focals relatively shyer than their second partner (shy focals). Results based on the absolute boldness scores were qualitatively similar. As our dataset consists of batches in two subsequent years we additionally ran all models with year as an extra fixed factor and found it had no significant effect in any of the models. The residuals for all models were visually inspected to ensure homogeneity of variance, normality of error and linearity. Finally, paired t-tests were used to investigate how the risk-taking behaviour of bold and shy focals changed across the isolation and two pairing stages. Repeatability across the six days of the experiment was estimated following the method by Lessells & Boag (1987). All results with $0.10 > p > 0.05$ are reported as trends and $p \leq 0.05$ as significant. Means are quoted ± SE throughout.

4.3 Results

We focus on the data collected during the second pairing and investigate how the personalities of the previous and current partner affect the behaviour of focal fish bolder than their current partner (bold focals) and focal fish shyer than their current partner (shy focals). The relative boldness of focal fish ranged from -0.62 for shy focals to +0.50 for bold focals (mean ± SE = -0.09 ± 0.03).

Time spent out of cover

Bold focals spent more time out of cover the bolder they were themselves (Figure 4.2A) but also the shyer their previous partner had been ($F_{2,7}$= 18.77, p = 0.002; Table 4.1), together explaining more than 80% of the variance (R^2 = 0.84). The personality of their current partner had no effect on the time bold focals were out of cover ($F_{1,7}$ = 0.04, p = 0.84). By contrast, shy focals tended to spend more time out of cover the bolder their current partner ($F_{1,22}$ = 4.11, p = 0.055; R^2 = 0.16), while their own personality ($F_{1,22}$ = 0.33, P = 0.571; Figure 4.2B) and that of their previous partner ($F_{1,22}$ = 0.04, p = 0.845) had no significant effect.

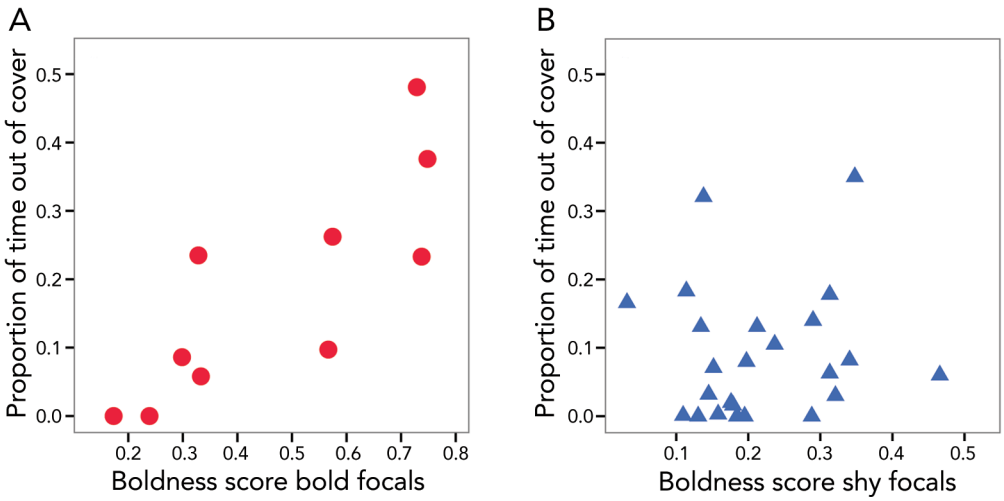

Figure 4.2 The proportion of time focal fish spent out of cover during the current pairing was (**A**) positively correlated with the boldness scores of bold focals (n = 10), but (**B**) not significantly correlated with the boldness scores of shy focals (n = 24). Boldness scores were square-root transformed.

Number of trips

The number of solo trips, when focal fish went out and returned to cover without being followed by their partner, was relatively higher in bold compared to shy focals (t = 2.56, p = 0.028; 13.8 ± 4.24 and 2.65 ± 1.02 trips respectively). Bold focals went on more solo trips the bolder they were themselves ($F_{1,8}$ = 6.60, p = 0.033; R^2 = 0.45) while the personality of the

current partner and the previous partner had no effect on this behaviour ($F_{1,7} = 0.09$, $p = 0.777$; $F_{1,7} = 1.67$, $p = 0.237$ respectively; Table 4.1). The number of solo trips made by shy focals was not explained by either their own personality ($F_{1,22} = 0.17$, $p = 0.687$), that of their current partner ($F_{1,22} = 0.25$, $p = 0.624$) or that of their previous partner ($F_{1,22} = 0.11$, $p = 0.743$).

There was no significant difference in the number of joint trips led by bold and shy focal fish during the second pairing ($t = 1.31$, $P = 0.211$; 7.15 ± 2.14 and 3.96 ± 1.19 trips respectively). Bold focals led more trips the relatively bolder they were (Figure 4.3A) but also the shyer their previous partner had been ($F_{2,7} = 12.98$, $p = 0.004$; Figure 4.3B; Table 4.1), together explaining 79% of the variance. The personality of the current partner did not affect the number of leadership trips for bold focals ($F_{1,6} = 1.53$, $p = 0.262$). By contrast, shy focals led more trips the bolder their current partner ($F_{1,22} = 5.75$ $p = 0.025$; $R^2 = 0.21$), while their own personality ($F_{2,21} = 0.28$, $p = 0.600$) and that of their previous partner ($F_{2,21} = 0.13$, $p = 0.719$) had no effect.

There was no significant difference in the number of trips bold and shy focals followed their current partner out of cover ($t = 1.91$, $p = 0.083$; 7.15 ± 2.14 and 2.91 ± 2.45 trips respectively). Bold focals followed their partner more the bolder it was (Figure 4.4) and the shyer their previous partner had been ($F_{2,7} = 41.74$, $p < 0.001$; Table 4.1), together explaining 92% of the variance. Bold focal's own personality did not play a role ($F_{1,6} = 2{,}28$, $p = 0.182$). Shy focals followed more the bolder their current partner was ($F_{1,21} = 7.78$, $p = 0.011$; Figure 4.4; $R^2 = 0.26$), with no effect of their own personality ($F_{1,21} = 0.60$, $p = 0.448$) and that of their previous partner ($F_{1,21} = 0.39$, $p = 0.537$).

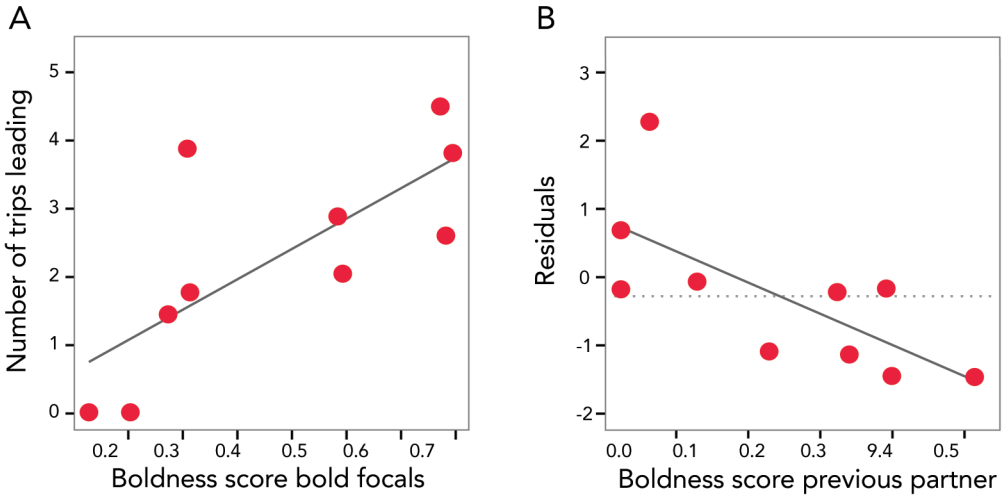

Figure 4.3 The number of trips bold focals ($n = 10$) initiated and were joined by their partner during the current pairing was (**A**) positively related to their own boldness score and (**B**) negatively related to the boldness score of their previous partner. The y-axis of plot b shows residuals of the model on leading trips with focal boldness score as the only factor. Scores above 0 indicate individuals were joined more than may be expected based on their own boldness score and scores below 0 individuals were joined less than may be expected based on their boldness score. Boldness scores and number of leading trips were square-root transformed.

Behavioural consistency across the stages

Bold focals were highly repeatable in the time they spent out of cover on the six days across the three stages (ICC = 0.76, 95% CI: 0.55 - 0.92), while shy focals were not (ICC = 0.17, 95% CI: 0.05 - 0.35). On average, bold focals spent similar amounts of time out of cover during the isolation stage and the first pairing (t_9 = 1.81, p = 0.104) but tended to spend less time out of cover during the second pairing compared to the isolation stage (t_9 = 2.18, p = 0.058). By contrast, shy focals spent more time out of cover when they could see their partner compared to when in isolation (first pairing: t_{31} = -2.29, p = 0.029; second pairing: t_{31} = -2.62, p = 0.013). Additionally, looking at focals based on their absolute boldness category (with bold fish spending more time out and shy fish less time out than the average focal fish) we found bold fish (ICC = 0.65, 95 % CI: 0.47 - 0.82) were more consistent than shy fish (ICC = 0.17, 95 % CI: 0.04 - 0.39), as reflected by their non-overlapping confidence intervals.

Table 4.1 Linear models of proportion of time out, number of solo trips, number of led trips, and number of trips followed by bold and shy focal fish

	Bold focals				Shy focals			
	Estimate	SE	*F*	*p*	Estimate	SE	*F*	*p*
Proportion of time out								
Constant	0.10	0.10		0.391	0.05	0.10		0.662
Personality focal	0.80	0.16	23.80	0.002	0.03	0.37	0.01	0.939
Personality current partner	0.07	0.32	0.04	0.844	0.45	0.22	4.11	0.055
Personality previous partner	-0.46	0.19	6.01	0.044	-0.03	0.15	0.04	0.847
Nr of solo trips								
Constant	-0.05	1.33		0.974	1.16	0.24		< 0.001
Personality focal	6.61	2.57	6.60	0.033	-1.01	2.47	0.17	0.687
Personality current partner	-1.48	5.04	0.08	0.777	0.78	1.57	0.25	0.624
Personality previous partner	-3.72	2.88	1.67	0.237	0.35	1.05	0.11	0.743
Nr of led trips								
Constant	1.18	0.78		0.174	-0.09	0.72		0.899
Personality focal	4.28	1.23	12.13	0.010	-1.37	2.56	0.28	0.600
Personality current partner	2.62	2.12	1.53	0.262	3.71	1.55	5.75	0.025
Personality previous partner	-3.88	1.39	7.79	0.027	0.38	1.05	0.13	0.719
Nr of followed trips								
Constant	1.05	0.47		0.062	-0.08	0.72		0.917
Personality focal	1.63	1.08	1.51	0.182	-1.96	2.53	0.60	0.447
Personality current partner	11.73	1.41	68.84	< 0.001	4.30	1.54	7.78	0.010
Personality previous partner	-2.93	1.06	7.51	0.029	0.65	1.04	0.39	0.537

These analyses looked at focals that were bolder than their final partner (n = 10) and focals that were shyer than their final partner (n = 24). Statistics for significant terms, shown in bold, were derived from the minimal model containing only significant terms while statistics for non-significant terms were obtained by running the minimal model with the term added individually. Coefficient estimates represent the change in the dependent variable relative to the baseline category and can therefore be interpreted as measures of effect size. All personality scores and response variables were square-root transformed.

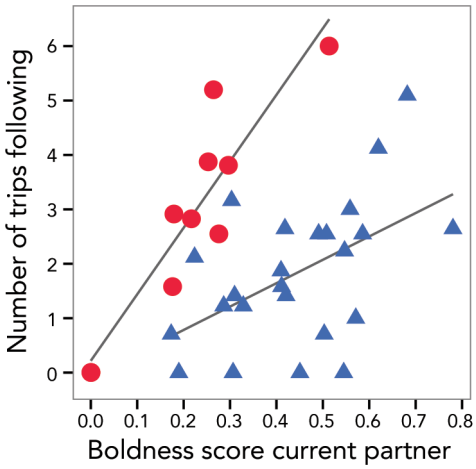

Figure 4.4 The number of trips focals went out of cover and joined their partner (following) during the current pairing is positively related to the boldness score of the current partner, both for bold focals (n = 10, circles) and shy focals (n = 24, triangles). Boldness scores and the number of following trips were square-root transformed. Two data points of the bold focals overlap at the origin because they both never followed and had a partner with a boldness score of 0.

4.4 Discussion

In this study, we show for the first time that the effect of the personality of a previous social partner can carry over to later social interactions, modulating the willingness of individuals to go out of cover and lead their partner. By contrast, the tendency to follow was mainly affected by the personality of an individual's current partner. Although bolder fish were more consistent than shyer fish in the time they spent out of cover across the contexts, it was only bold fish that were susceptible to social reinforcement by their previous social interactions. Shyer fish behaved much more flexibly and responded most strongly to their current partner.

Previously, some studies have shown that previous social experience may affect neophobia and aggression (Hsu & Wolf, 1999; Frost et al., 2007), and that experience within the same pair may override personality differences in leadership tendencies (Nakayama et al., 2013). Here we show for the first time how social experiences with previous partners may affect later leadership behaviour: the bolder their previous partner, the relatively less time bold focals spent out of cover, making them less successful in taking the lead. These findings help answer the important question in the leadership literature of what makes an initiator successful in triggering collective movement (Petit & Bon, 2010). Although bolder individuals are less sensitive to failure in recruiting a partner, they are responsive to their partner's behaviour when it has taken on the role of leader. This may be especially the case when bold focals are paired with a relatively bold partner. In such a situation, the partner is relatively more likely to take the lead compared to a shyer partner. Consequently, the focal individual may be less likely to be followed, resulting in a reduction of positive feedback in leadership and reduced performance in the pair (Nakayama et al., 2013). Such experience may then subsequently

modulate focal fish' willingness to go out of cover and lead their partner. Not only does this finding highlight that bolder individuals may be more susceptible to social reinforcement than shy individuals, it indicates that for leadership social experience is important. To be an effective leader, an individual may need experience with good followers, providing positive social feedback and leading experience, and ultimately more successful leadership. These findings may have potential for our understanding of human leadership, as a lack of knowledge of the social dynamics underlying leadership has been highlighted in the social sciences (Amit et al., 2009; Emery, 2010; DuBrin, 2013). Future studies could look in more detail at the extent of the difference in personality scores between the partners and determine the effect it may have on collective behaviour.

The finding that bold but not shy focals were affected by a previous partner might be explained by the fact that shyer individuals are in general more sociable (Ward et al., 2004; Pike et al., 2008) and more flexible in their behaviour (Nakayama et al., 2012b), than bold individuals. Indeed, we found that the current partner's personality explains much more of shy focals' behaviour than that of bold focals, in line with previous studies reporting that shy individuals are more responsive to the actions of their (current) group members (Pike et al., 2008; Nakayama et al., 2012a,b). This may also explain the more general finding that shy but not bold focals spent considerably more time out of cover when there was a conspecific present compared to when they were in isolation. Interestingly, in contrast to the time spent out of cover and leading behaviour, following behaviour of both bold and shy focals was primarily explained by the boldness of their current partner. This result is in line with a number of recent studies that have shown that both bold and shy individuals are responsive when in the following position (Nakayama et al., 2012a,b), and that experience may override personality differences in the tendency to follow but not in the tendency to lead (Nakayama et al., 2013). Together, these findings thus suggest that regardless of an individual's own personality, its tendency to follow mainly depends on the behaviour of its current partner(s). Leadership, in contrast, is particularly dependent on a bolder personality type, with a modifying effect of social feedback from previous experiences.

Overall, our findings demonstrate a general difference in responsiveness between shy and bold individuals. Although both bold and shy individuals adjusted their behaviour, bold individuals were more consistent in their behaviour than shy individuals. That they adjusted their behaviour based on their previous partner suggests social reinforcement. In contrast, shy individuals mostly adjusted their behaviour based on their current partner. These results support two recent theoretical models that showed how a co-evolutionary process between responsiveness and consistency may eventually result in populations that consist of highly responsive individuals that follow and behaviourally consistent individuals that mainly lead (Wolf et al., 2011; Johnstone & Manica, 2011). Furthermore, these findings are highly relevant in the light of the idea that individual differences can be seen as behavioural specializations (Dall

et al., 2012). If individuals differ in the extent that they change their behaviour based on previous and current experiences, this represents a potential mechanism through which social roles can be generated and reinforced to create even longer lasting differences between individuals. In other words, personality differences may be maintained in populations because of their role in social coordination (see also King, Johnson, and Van Vugt 2009).

Whilst the study of collective behaviour, from pairs of individuals to groups of thousands of individuals, was initially mostly focused on homogeneous interaction rules (Couzin & Krause, 2003; Petit & Bon, 2010; Vicsek & Zafeiris, 2012), individual differences are increasingly taken into account when examining group behaviour (Conradt & List, 2009; Herbert-Read et al., 2012; Jolles et al., 2013b). Here we go one step further by showing that social dynamics across time and social contexts may have a considerable effect on individual and thereby group behaviour. Our study is the first to demonstrate that leadership roles are affected by social experiences from previous partners and that this depends on an individual's personality, with bold but not shy fish being affected by the personality of a previous partner. These findings help understand how leading and following behaviour emerge and are maintained and highlight the important influence current as well as previous social experiences can have on individual and collective behaviour.

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Chapter 5

The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks

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Abstract

Social animals must time and coordinate their behaviour to ensure the benefits of grouping, resulting in collective movements and the potential emergence of leaders and followers. However, individuals often differ consistently from one another in how they cope with their environment (animal personality), which may affect how individuals use coordination rules and requiring them to compromise. Here we tracked the movements of pairs of three-spined sticklebacks, *Gasterosteus aculeatus*, separated by a transparent partition that allowed them to observe and interact with one another in a context containing cover. Individuals differed consistently in their tendency to approach their partner's compartment during collective movements. The strength of this social attraction was positively correlated with the behavioural coordination between members of a pair but was negatively correlated with an individual's tendency to lead. Social attraction may form part of a broader behavioural syndrome, as it was predicted by the boldness of an individual, measured in isolation prior to the observation of pairs, and by the boldness of the partner. We found that bolder fish and those paired with bolder partners tended to approach their partner's compartment less closely. These findings provide important insights into the mechanisms that govern the dynamics and functioning of social groups and the emergence and maintenance of consistent behavioural differences.

5.1 Introduction

Social animals may benefit from grouping due to reduced predation risk, earlier predator detection and greater foraging success (Pitcher & Parrish, 1993; Krause & Ruxton, 2002). At the same time, grouping may entail costs in the form of increased competition and predator attraction (Krause & Ruxton, 2002). To ensure that individuals reap the full benefits of grouping, they must coordinate their behaviour with other group members (Vugt, 2006; Conradt & Roper, 2009), resulting in collective movements and decisions (Couzin et al., 2011; Miller et al., 2013) and the possible emergence of leaders and followers (Krause & Ruxton, 2002; King et al., 2009). Focus on the mechanisms that govern such collective behaviour may increase our understanding of the social organization and dynamics within and across groups, from aggregating insects to human societies (Conradt & List, 2009; King et al., 2009).

Group movements and decisions can often be explained by individuals following simple rules (Couzin & Krause, 2003; Couzin et al., 2005; Sumpter, 2006). However, individuals often behave consistently different from one another, now mostly referred to as animal personality (Sih et al. 2004; Réale et al. 2007, 2010), with large potential consequences for the functioning and structure of social groups (Wolf & Krause, 2014). Particularly relevant in the context of collective behaviour is boldness, i.e. individual variation in the tendency to take risks. Bolder individuals may be more likely to lead, so as to maximise their foraging opportunities (Chapter 6; Biro & Stamps, 2008; Kurvers et al., 2010b; Jolles et al., 2013b), whereas shy individuals may be more likely to group (Bell & Sih, 2007) and respond to conspecifics (Pike et al., 2008; Croft et al., 2009; Harcourt et al., 2010a; Kurvers et al., 2010a; Trompf & Brown, 2014) for anti-predator benefits (Krause & Ruxton, 2002). Although previous work has confirmed that bolder individuals are more likely to take the lead and shy individuals are more likely to follow (Chapter 4; Harcourt et al., 2009; Kurvers et al., 2009; Nakayama et al., 2012a), the impact of boldness on social attraction during collective movement remains unclear.

Previous work that focused on the tendency for individuals to be attracted to others, i.e. sociability, has revealed large ecological and evolutionary implications (Cote & Clobert, 2007; Réale et al., 2007; Cote et al., 2010). Also in the context of collective behaviour (Dingemanse & Réale, 2005; Réale et al., 2007; Cote et al., 2012), sociable individuals have more and stronger social associations (Croft et al., 2009), have stronger grouping preferences (Cote et al., 2012), and play a key role in group exploration (Brown & Irving, 2014). However, studies typically measure the tendency of individuals to approach a static group of conspecifics or a larger over a smaller one (see Wright & Krause, 2006). Not only is this less relevant to the natural situation, where individuals can interact and respond to one another (see also Miller & Gerlai, 2007), but also the mechanistic role of social attraction in coordination and leadership and the potential effects of social feedback remain unclear (Miller & Gerlai, 2008; Wilson et al., 2013). For example, sociability may be linked to the distance-regulation between individuals (Pitcher &

Parrish, 1993; Krause et al., 2000), and thereby affect leading and following behaviour. Our aim in this study was to explore social attraction, i.e. the tendency for individuals to approach a partner, in the context of joint movement of pairs of stickleback fish. This allowed us to assess the impact of social attraction on collective behaviour and look at the role played by social feedback in a similar way to recent studies on boldness and leadership (Chapter 4; Ward et al., 2013; Pettit et al., 2013; Nakayama et al., 2013).

We repeatedly observed three-spined sticklebacks, *Gasterosteus aculeatus*, in a context in which they could rest under cover or explore an open, potentially risky environment. We first assessed the boldness of all fish by recording their behaviour in isolation, after which we subjected them to the same environment again but this time allowing observation of a conspecific through a transparent partition. By tracking the movements of both fish in and out of cover and determining their tendency to approach their partner's compartment we aimed to determine (1) whether individuals are consistent in the strength of social attraction they exhibit in an ecologically relevant setting, (2) what link may exist between the tendency for social attraction and boldness, (3) whether social attraction is influenced by the personality of a partner as well as that of the focal individual and (4) how social attraction varies during collective movements (when both fish are out of cover) compared to when fish are out alone, either during the initiation and return of such movements or during solitary trips. This approach of subjecting fish to a dynamic social context in which they can move with conspecifics as well as rest under cover provides a unique opportunity to describe important new aspects of sociability and risk-taking behaviour and their role in the mechanisms underlying collective behaviour.

5.2 Methods

Overview

Ninety-six fish were tested repeatedly in a task in which they could either rest under cover or explore an open, potentially risky environment (risk-taking task). Two such task compartments were positioned adjacent to one another and separated by either an opaque or a transparent partition (see Figure 5.1). First, we tested fish individually in the compartments separated by an opaque partition to investigate their propensity to explore a risky area when alone ('isolation stage'). Second, we tested fish in the risk-taking task again but now with the compartments separated by a transparent partition, thus allowing fish to see each other and interact ('pairing stage'). By testing fish twice in each stage we were able to get individual consistency scores of risk-taking behaviour when alone (boldness) and their tendency to approach the partner's compartment when together (social attraction). Third, we tested an additional 16 fish using the same procedure as above, but with a transparent instead of an

opaque partition, and an empty adjacent compartment during the isolation stage. This allowed us to ensure differences in behaviour between the two stages were not simply due to the transparency of the partition.

Subjects and housing

We collected three-spined sticklebacks during the summers of 2010–2012 using a sweep net from a small branch of the River Cam (Cambridge, UK). Fish were taken from a single population to minimise population-specific genetic effects that may influence personality (Bell, 2005). After collection, fish were immediately housed in a temperature-controlled laboratory (14 ± 1 °C) with constant light regime (lights on from 0900 to 1900 hours), and kept in large, glass social-housing tanks (120 cm length × 60 cm width × 60 cm high) with artificial plants, aeration and under-gravel filtration. During this period before experiments, fish were fed frozen bloodworms (*Chironomidae* larvae) *ad libitum* once daily. As the temperature and photoperiod regime in the laboratory prevented the fish from becoming sexually mature (Borg et al., 2004), we did not sex the fish.

We performed our experiments with four batches of fish (n = 96 total), which were about 6 months old at the time of testing. After an acclimatization period of at least 1 month, for each batch we randomly selected fish from the social-housing tanks controlling for size (mean ± SE: 44 ± 1 mm from tip of snout to caudal peduncle). Fish were subsequently housed in custom holding tanks (60 cm × 30 cm × 40 cm) lined with gravel and divided lengthwise into six compartments (30 cm × 12 cm; 15 cm deep). Five of the compartments contained an artificial plant; the remaining compartment contained an under-gravel filter and was not used to house fish. Fish were randomly allocated to compartments. To minimise potential stress effects that may be caused by isolation, the compartments were divided by perforated transparent Perspex partitions, thus allowing fish to receive chemical and visual cues from conspecifics. After the experiments, fish were kept in the laboratory and used for additional behavioural experiments. Animal care and experimental procedures were approved by the Animal Users Management Committee of the University of Cambridge under a non-regulated procedures regime because of the nonintrusive and observational nature of our work.

Experimental set-up

To investigate fish's willingness to take risks as well as their tendency to approach conspecifics during collective behaviour, we used a tank set-up as previously used in our laboratory for similar experiments (Chapter 4; Harcourt et al., 2009; Nakayama et al., 2012a). In short, experiments were carried out in four identical experimental tanks (70 cm × 30 cm ×30 cm), each divided by either an opaque or a transparent Perspex partition to create two long compartments (15 cm wide). Each compartment was lined with gravel in a slope ranging from a deep area (14 cm deep) that contained an artificial plant to an increasingly shallow 'exposed'

area (4 cm deep at the other side, see Figure 5.1A). Only when fish had fully emerged from the deep 'covered' area (15 cm from the back of the compartment) did we define them to be 'out of cover'. This set-up reflects the ecologically relevant situation in which fish can either rest in a safe place or explore a risky area (in search of potential food). Fish prefer to spend time under cover but, even in the absence of food, keep making regular trips out of cover to explore the exposed area. Fish have different preferences for how frequently and for how long they leave cover, yet try to coordinate their behaviour and shoal together, generating a conflict on the timing of leaving and returning to cover. Although the partition prevented the transfer of chemical cues, fish could see and interact with one another when we used the transparent partition. The other three sides of the compartments were covered by white Perspex to minimise any outside disturbances. When we were not running experiments, the water of the experimental tanks was oxygenated using air stones. An HD camera (Camileo X100, Toshiba Corporation, Japan) positioned above each tank was used to record the movements of the fish.

Experimental procedure

The first three days of the experimental period were used to acclimate the fish to their individual housing tanks. Subsequently, on the next two days, fish were tested for one hour per day in the compartments separated by an opaque partition ('isolation stage'). This allowed us to get a boldness score for each fish: consistency in the proportion of time out of cover. After a rest day, fish were again tested in the compartments for two days, one hour per day, but now with the compartments separated by a transparent partition, thus allowing fish to see each other and interact ('pairing stage'). Fish in adjacent compartments were the same for both days of the pairing stage. This testing of fish in 'pairs' allowed us to get social attraction scores for each fish based on their tendency to approach their partner's compartment (see Data analysis for details), and enabled us to investigate the link between boldness and social attraction and their role during solitary and collective behaviour.

For each session, fish were transferred to the deep end of the tank using a dip net and allowed to acclimate for 7 min before we filmed their movements. Fish were tested in a random order and were randomly assigned to tank and compartment in the tank. To avoid non-independence in our analyses, we randomly selected one fish in each pair (n = 48) as the focal individual and the other as its partner. During the experimental period fish were fed one bloodworm at the end of each day to standardise hunger levels. No food was provided during the experimental sessions and fish were thus not rewarded for leaving cover.

To ensure that any differences in behaviour between the isolation and pairing stages were not simply a response to the transparent partition itself (but rather the result of interactions between the two fish), we ran an additional control condition with naïve fish (n = 16). This 'transparency control' followed the same procedure as the main experiment (see above), but now during the isolation stage randomly selected focal fish (n = 8) were tested in a

compartment separated by a transparent partition and with no fish in the adjacent compartment.

Video tracking

From the videos, we determined the exact position of all fish 10 times/s using automated motion-tracking software (AnTracks version 0.99, www.antracks.org), providing us with X and Y coordinates of each fish over time on a mm scale. For tracking, we used a background subtraction acquisition method that determines which pixels differ between a video and a background image created from a random 5 min period in each recording. For processing, we used Gauss subtraction, Gauss blur, dilate and final thresholding, with the parameters adjusted according to the light levels in each video to ensure the movements of the fish were tracked correctly. After tracking was complete, we visually checked all trajectories for each video, manually correcting any errors and joining discontinuous trips where the software had lost track of a fish for a few frames.

Data analysis

Data were analysed in R 3.0.2 (The R Foundation for Statistical Computing, Vienna, Austria). The positional coordinates of each fish were used to calculate the timing and proportion of time fish were out of cover and, as a proxy for social attraction, the fish's average distance to the partner's compartment (see Figure 5.1A). To avoid non-independence, the majority of analyses focused on the behaviour of the randomly predetermined focal fish, with certain analyses incorporating the personality of the partner (see below).

First, we quantified boldness, social attraction and coordination. Boldness scores were calculated as the average proportion of time individuals spent out of cover on both days of the isolation stage; and we confirmed that this was consistent using a Spearman rank correlation test. Previous work with the same experimental set-up has established that this behaviour is consistent over longer periods of time (Harcourt et al., 2009). A social attraction score was calculated as the average distance from the adjacent compartment during collective movements. To determine whether fish swam on average in the middle of their compartment, we used one-sample *t* tests and one-sample Wilcoxon signed-rank tests. To get a measure of coordination within the pair, we used the same logic as used for estimating genetic linkage (Rands et al., 2008; Harcourt et al., 2009), with scores reflecting the proportion of time both fish in a pair carried out the same behaviour relative to the time they carried out opposite behaviours.

Second, to determine whether fish changed their behaviour between the isolation and pairing stages, we used Wilcoxon signed-ranks tests and paired *t* tests, and we used a Spearman rank correlation test to investigate whether the change in risk-taking behaviour between the stages was linked to initial risk-taking behaviour. To compare social attraction of

focal fish from the main experiment with fish from the transparency control group, we used an Independent Samples *t* test. Furthermore, as previous work has shown that the relative boldness of fish is important in social interactions (Harcourt et al., 2009; Nakayama et al., 2013), we compared the social attraction of focal fish that were bolder ('bold focals') and focal fish that were shyer than their partner ('shy focals'). The relative boldness of focal fish to their partner ranged from -0.60 to +0.56 (shy focal fish: $n = 15$; bold focal fish: $n = 14$; mean ± SE = -0.03 ± 0.03). We excluded cases in which neither the focal fish nor its partner went out of cover during the isolation stage, and when the focal fish did not go out of cover during the pairing stage as then no social attraction score could be calculated.

Third, to determine the role of boldness in risk-taking behaviour and social attraction during the pairing stage, we ran linear models with, respectively, the proportion of time spent out of cover (risk taking) and mean distance from the central partition (social attraction) by the focal individuals as response variables. As predictors, we fitted the boldness score of the focal individual, the boldness score of its partner and the interaction between them. To investigate how the overall social attraction of both fish in a pair affected their coordination, we ran a Spearman rank correlation; to determine its role in leadership behaviour we ran a linear model with, as response variable, the number of trips on which the focal individual led its partner, and the social attraction score of the focal fish and its partner as predictors. Leading was defined as the focal fish leaving cover and subsequently being joined by its partner. Minimal adequate models were obtained by backward stepwise elimination (i.e. sequentially dropping the least significant terms from the full model, until all terms in the model were significant). Statistics for non-significant terms were obtained by adding each non-significant term to the minimal model. Boldness and social attraction scores were square-root transformed to ensure homogeneity of variance, normality of errors and linearity.

Fourth, to further understand the dynamics behind social attraction, we investigated an individual's tendency to approach its partner's compartment both during 'collective movements', i.e. when both fish were out of cover and when fish were out alone. Fish could be out of cover alone during (1) the 'initiation' of collective movement: the focal fish left cover but was not joined by its partner; (2) the 'return' of collective movements: when the focal fish was still out after collective movement but the partner was already back in cover; and (3) 'solo trips': when the focal fish was out of cover and returned to cover without the partner coming out. We used paired *t* tests and Wilcoxon signed-ranks tests to compare social attraction across these different stages of collective movement. As body size did not have a significant effect on any of the measured behaviours and was not the focus of the present study, we have excluded it from our results. All results with $p < 0.10$ are reported as trends and $p < 0.05$ as significant. Means are quoted ± SE throughout.

5.3 Results

Risk-taking behaviour

Fish were highly consistent in the proportion of time spent out of cover during the isolation stage ($r_s = 0.65$, $p < 0.001$, $n = 96$), providing the boldness score for each fish. Focal fish spent on average a similar amount of time out of cover during the isolation stage (0.10 ± 0.02) and the pairing stage (0.12 ± 0.02; $V = 388$, $p = 0.145$). However, there was a negative relationship between the initial time focal fish spent out of cover (i.e. their boldness) and their change in risk-taking behaviour across the stages ($r_s = -0.37$, $p = 0.010$, $n = 48$): bolder fish spent less time and shy fish more time out of cover during the pairing stage. The proportion of time focal fish spent out of cover during the pairing stage was predicted by a negative interaction between their own boldness and that of their partner ($F_{3,44} = 9.22$, $p = 0.008$, $R^2 = 0.39$): although bolder fish spent in general more time out of cover than shyer fish, having a relatively bold partner decreased this difference between bold and shy fish.

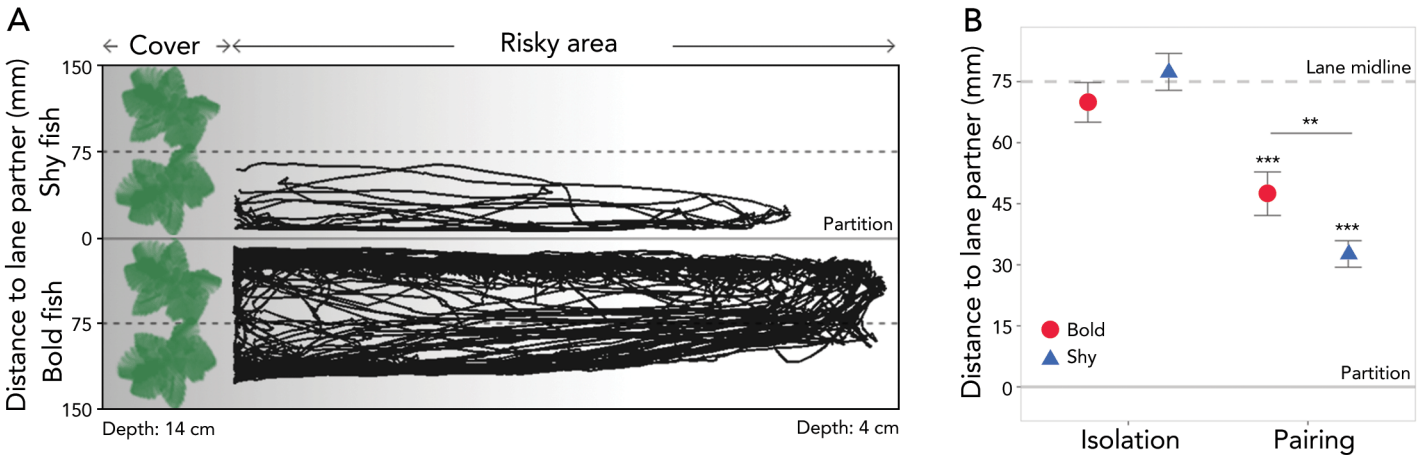

Figure 5.1 (**A**) Schematic overview of the experimental tank with a transparent partition, with all movement trajectories (black lines) of a representative pair of fish when not in the cover area (15 cm length) during the first day of the pairing stage. (**B**) Distance to the partner's lane (mm) for focal fish bolder and shyer than their partner during the isolation ($n = 19$; $n = 19$) and pairing stages ($n = 14$; $n = 15$). ** $p < 0.01$; *** $p < 0.005$.

Social attraction: stage comparisons

Focal fish swam on average in the middle of their compartment when in isolation (1.35 ± 3.35 mm; $t_{37} = -0.41$, $p = 0.688$; Figure 5.2 and Figure 5.3), but were on average much closer to their partner's compartment (39.1 ± 3.1 mm away; 35.9 mm from the middle) when paired ($t = 6.47$, $p < 0.001$). During the pairing stage, shy focal fish swam much closer to the adjacent compartment than bold focal fish ($t_{23.74} = 4.05$, $p = 0.003$; Figure 5.1B). These results were not simply a consequence of the different partitions used in the isolation and pairing stages. Fish

from the transparency control group, which were tested with a transparent partition and an empty adjacent compartment during the isolation stage, swam on average in the middle of their lane during the isolation stage (0.4 ± 7.6 mm; $t_5 = 0.04$, $p = 0.969$). Their distance from the partition was not significantly different from the distance kept by focal fish during the isolation stage of the main experiment with an opaque partition ($t_{7.1} = -0.20$, $p = 0.847$). Furthermore, during the pairing stage, fish in the control group swam closer to the partition than during the isolation stage ($t_4 = 5.43$, $p = 0.006$), even though they had a transparent partition throughout.

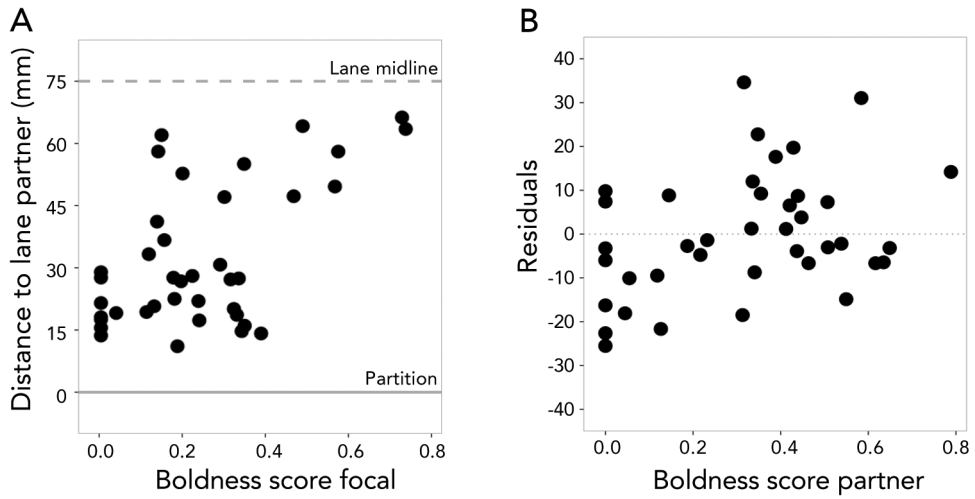

Figure 5.2 Focal fish' distance to their partner's lane (mm) in relation to (**A**) their own boldness and (**B**) the boldness of their partner during collective movements in the pairing stage. Boldness scores are square-root transformed.

Social attraction: collective states

During the pairing stage, fish in adjacent compartments (a 'pair') could be in different collective states: focal fish and their partner could both be out of cover (collective movement) or focal fish could be out alone during the initiation of these collective movements (initiation), during the return of these trips terminated by the partner (return) and during solitary trips (solo trip). During collective movements, focal fish stayed close to their partner's compartment, on average swimming 32.2 ± 2.7 mm from the transparent partition, and were consistent in their tendency to do so across both days ($r_s = 0.48$, $n = 22$, $p = 0.024$), providing the social attraction score for each fish. Social attraction was negatively related to the focal fish's own boldness ($F_{1,37} = 20.82$, $p < 0.001$) as well as that of their partner ($F_{1,37} = 5.67$, $p = 0.023$; full model: $F_{2,37} = 11.55$, $p < 0.001$; $R^2 = 0.39$; Figure 5.2). In other words, bolder fish or fish paired with a bolder partner were less inclined to swim near the partition separating the two compartments. Furthermore, the boldness of the partner had a positive effect on the total number of collective movements (i.e. trips when both fish were out together; $r_s = 0.45$, $n = 48$, $p = 0.001$). The average distance of focal fish to their partner's compartment did not differ

significantly between trips initiated by the focal fish (i.e. when leading; 37.7 ± 4.4 mm) and those initiated by their partner (i.e. when following; 33.9 ± 3.2 mm; $t_{34} = 0.69$, $p = 0.494$).

When focal fish were out of cover alone, their average position was still significantly different from the middle of their lane and closer to the partner's compartment (49.9 ± 4.7 mm; $t_{39} = -5.34$, $p < 0.001$). This tendency to approach the partner's compartment when focal fish were out of cover alone was negatively related to their own boldness ($F_{1,38} = 11.67$, $p = 0.002$, $R^2 = 0.24$), but, in contrast to the results obtained for collective movements, not related to the boldness of their partner ($F_{1,38} = 1.60$, $p = 0.214$).

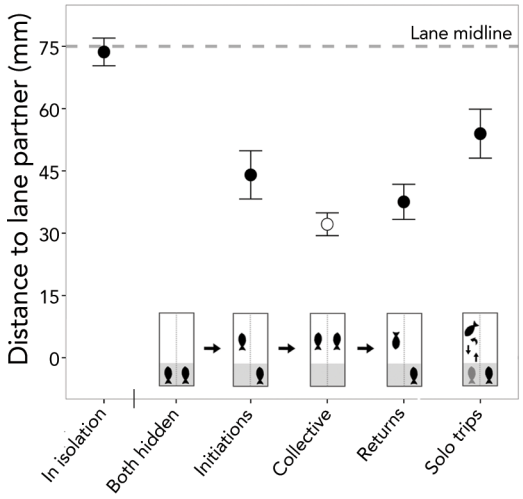

Figure 5.3 Plot showing the distance of focal fish to the lane of their partner (mm) during the isolation stage when out of cover, and during the pairing stage, separate for each of four possible states in which focal fish could be out of cover: when focal fish initiated trips later joined by their partner (initiations), when focal fish and their partner were out together (collective movements), when focal fish were still out of cover after a collective trip but their partner was already back under cover (returns) and focal fish going out and back under cover during solo trips. The distance of focal fish to their partner's lane during collective movements is depicted in white.

Looking at the average lateral position of focal fish (the position relative to the partition separating the compartments), there was no significant difference in position during collective movement and the return from such movements ($V = 340$, $p = 0.478$; Figure 5.3). However, focal fish tended to be further away from their partner's compartment during the initiation of collective movements ($V = 407$, $p = 0.062$; Figure 5.3) and during solo trips ($V = 435$, $p < 0.001$; Figure 5.3). Focal fish swam significantly closer to their partner's compartment when initiating collective movements than when on solo trips ($V = 315$, $p = 0.035$; Figure 5.3). Even when we restricted our analysis to the first 10 cm out of cover, which was the average distance focal fish moved before being joined by their partner, we still found a trend for this effect ($V = 303$, $p = 0.066$). Focal fish swam significantly less far out of cover when they went out of cover alone on a solo trip (22.3 ± 2.0 cm) than when their partner was also out (i.e. during collective movements; 28.4 ± 1.3 cm; $t_{32} = 4.95$, $p < 0.001$).

Collective behaviour

Compared to the isolation stage, when fish in adjacent compartments were rarely out together (4.2 ± 1.0% of time out), during the pairing stage, when fish in adjacent compartments could see and interact with one another through the transparent partition, fish spent considerably more time out together (26.9 ± 3.4% of time out; $V = 75$, $p < 0.001$). Furthermore, during the pairing stage fish had higher behavioural coordination with one another (0.74 ± 0.04; $V = 230$, $p = 0.006$) than when they were tested in isolation (0.59 ± 0.04). Pairs that had higher overall social attraction (i.e. pairs in which both fish swam closer to one another during collective movements) showed more coordinated behaviour ($r_s = -0.38$, $p = 0.018$, $n = 39$), but tended to travel shorter distances out of cover ($r_s = 0.31$, $p = 0.052$, $n = 39$). More sociable individuals led fewer trips ($F_{1,37} = 7.96$, $p = 0.008$, $R^2 = 0.18$), with no effect of the sociability of the partner ($F_{1,36} = 0.79$, $p = 0.381$).

5.4 Discussion

By tracking the movements of interacting pairs of three-spined sticklebacks, we found that individuals varied consistently in the average distance they maintained from their partner's compartment during collective movements, an aspect of their behaviour that we refer to as 'social attraction'. Although less social individuals led more collective trips, pairs consisting of more social individuals showed higher behavioural coordination. The tendency for social attraction was negatively correlated with both the boldness of the focal fish and that of its partner, i.e. bolder fish with bolder partners stayed further away from their partner's lane, whereas shyer fish with shyer partners swam closer to it. Individuals that displayed stronger social attraction even persisted in swimming closer to their partner's lane when they were out of cover alone while their partner remained under cover. This result was not a consequence of using a transparent partition, since fish in the control group only swam closer to the transparent partition when the adjacent compartment contained another fish.

By investigating sociability behaviour in a dynamic social context, we have shown that social feedback plays a key role in social attraction tendencies and thereby affects group cohesion and coordination. Individuals with higher social attraction swam closer to one another, decreasing the distance between them (see also Cote et al., 2012), and because of the resulting positive feedback, became even more cohesive as a pair. At the same time, fish paired with bolder, less social partners increased their time spent out of cover (see also Chapter 4; Pike et al., 2008; Harcourt et al., 2009; Nakayama et al., 2012b), but showed lower social cohesion because of less social feedback when approaching their partner. Not only do these findings substantiate the importance of social feedback in collective behaviour, as previously shown for boldness and leadership (Chapter 4; Harcourt et al., 2009; Ward et al., 2013; Pettit et al., 2013;

Nakayama et al., 2013), they also support theoretical expectations about the consequences of personality differences for the functioning and structure of social groups (Wolf & Krause, 2014).

Our findings about the role of sociability expression in group coordination and cohesion are interesting in relation to leadership behaviour. Although pairs with higher overall social attraction had higher behavioural coordination, they tended to explore less far out of cover. Furthermore, individual social attraction was negatively correlated with the leadership tendencies of individuals. Previous studies have shown that bolder fish more often take the lead and that shyer fish more often follow (Chapter 4; Harcourt et al., 2009; Nakayama et al., 2013). Furthermore, bolder individuals often have fewer or weaker social interactions with conspecifics than do shyer conspecifics (Pike et al., 2008; Croft et al., 2009). Since boldness and social attraction were negatively linked in our study, our results suggest that bolder, less sociable individuals may often lead simply because they are less reluctant to move away from their partners, whereas shyer, more sociable, individuals become followers because they prioritise staying close to others (see also Couzin et al., 2005).

Our study is the first to show a direct negative impact of boldness on social attraction by assessing both in the same, ecologically relevant setting. This negative relationship is in line with previous work that examined sociability and boldness in separate contexts (e.g. Budaev, 1997; Ward et al., 2004; Croft et al., 2009; Pruitt et al., 2010; but see Cote et al., 2008, 2010; Irving & Brown, 2013), and supports the idea of a more general difference in sociality between bold and shy individuals (see Magnhagen, 2012). For example, bold individuals have been shown to group less (Bell & Sih, 2007), to interact less regularly with their group mates (Pike et al., 2008; Croft et al., 2009), and to be either less reliant on social information (Harcourt et al., 2010a; Kurvers et al., 2010a) or to use it more to avoid conspecifics (Trompf & Brown, 2014). Together, these findings suggest that sociability and boldness may represent different aspects of the same, fundamental behavioural syndrome (see also Cote & Clobert 2007; Sih et al. 2012), with potentially large ecological implications (Webster & Ward, 2011; Sih et al., 2012). Differences in boldness and sociability may be expressions of underlying risk-prone or risk-averse behavioural types, as risk-averse individuals may be more motivated to group and respond to conspecifics in order to lower their risk of predation (Krause & Ruxton, 2002). Together these findings show that differences in leadership behaviour may ultimately emerge from a combination of initial differences in the use of coordination rules and the resulting social feedback. This raises the intriguing idea that differences in personality between individuals may be maintained in populations because of their role in promoting social coordination (King et al., 2009; Johnstone & Manica, 2011).

To conclude, by tracking the movements of interacting pairs of fish in an ecologically relevant setting in which fish had to make decisions regarding exploration versus resting under cover, we have shown that social attraction, like leadership, is associated with individual

boldness, but is also subject to social feedback, being influenced by the personality of the partner as well as that of the focal individual. Further studies are needed to better understand how boldness and social attraction vary in larger, more dynamic groups and how the composition of behavioural types ultimately affects group functioning and success.

Acknowledgments

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Chapter 6

Personality differences drive collective behaviour and explain group functioning in schooling fish

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In preparation

Abstract

Collective behaviour patterns emerge when group members respond to each other's location and movements via simple interaction rules. Research has primarily focused on homogeneous groups and assumed individuals use identical interaction rules. However, the presence of clearly distinct behavioural tendencies (personalities) in many social species challenges this assumption. Here we investigate the role of personality variation in collective behaviour by detailed tracking of the movements and group foraging of free-swimming stickleback shoals for which the personality type of each member is known. We show that sociability and boldness have strong complementary driving effects on the spatial positioning and leadership of individuals, and together determine individual foraging success. Furthermore, we reveal that individual personality effects drive group cohesion, exploration, and polarisation, and thereby explain group foraging success. Finally, we show that in turn the group personality composition ultimately determines individual performance. Taken together, these results show personality variation is a fundamental aspect of collective behaviour and group functioning, and may help explain the evolutionary maintenance of personality variation.

Introduction

A fundamental problem in the natural sciences is understanding how collective behaviour and group decision-making result from the actions and interactions of individual group members (Sumpter, 2010). Complex collective behaviours, such as the flocking of birds and shoaling of fish, have been shown to arise from individual group members following relatively simple interaction rules (Couzin & Krause, 2003; Sumpter, 2006, 2010; Herbert-Read et al., 2011; Katz et al., 2011; Gautrais et al., 2012). Differences in state (e.g. energy reserve, knowledge) among individuals have been argued to provide an additional driver of collective behaviours (Krause et al., 2000; Conradt et al., 2009; Couzin et al., 2011), with rules mediating the effect of differences in state (Rands et al., 2003). However, most animal groups are comprised of individuals with considerably different behavioural tendencies, 'animal personalities' (Réale et al., 2007; Bell et al., 2009; Dingemanse & Wolf, 2010). This raises the question of whether the interaction of different personality types and the rules they follow might be an important layer of added complexity that should be accounted for to understand collective movements and decisions (Harcourt et al., 2009; Webster & Ward, 2011; Aplin et al., 2014; Wolf & Krause, 2014; Strandburg-Peshkin et al., 2015). This may also shed light on the evolutionary maintenance of personalities, an open question in behavioural ecology (Wolf & Krause, 2014; Farine, Montiglio & Spiegel, 2015).

By coordinating their behaviour (Herbert-Read et al., 2011; Katz et al., 2011; Gautrais et al., 2012), individual animals can reach and maintain group coherence and consensus (Couzin et al., 2005, 2011), providing individuals with important predation and foraging benefits (Pitcher & Parrish, 1993; Krause & Ruxton, 2002). However, costs and benefits are not shared equally (Krause & Ruxton, 2002; Couzin & Krause, 2003), as predation risk (Bumann et al., 1997; Krause et al., 2000) and food intake (Krause et al., 1998; Krause & Ruxton, 2002) are generally highest on the edge and in the front of animal groups. Theoretical work (Couzin et al., 2002; Couzin & Krause, 2003; Conradt et al., 2009) has demonstrated that already minor changes in individual behaviour may affect an individual's spatial positioning and strongly influence the movements of the group. For example, simply through variability in social attraction, more social individuals are predicted to move towards the centre of the group and less social individuals to the front (Couzin et al., 2002; Conradt et al., 2009). Furthermore, individuals are predicted to directly occupy such front positions when they more assertive (Conradt et al., 2009), and willing to accept higher risks, such as due to higher energy demands (Hoare et al., 2000; Krause et al., 2000; Conradt et al., 2009). As group movements are generally determined by individuals in the front of the group (Bumann & Krause, 1993; Krause et al., 2000), leadership is predicted to emerge both as a result of social indifference as well as according to need (Conradt et al., 2009), with potentially strong effects on foraging dynamics (Krause et al., 1998; Krause & Ruxton, 2002). As animals often vary consistently from one another in their tendency to approach others, i.e. their 'sociability', and their tendency to accept

risks for potential rewards, i.e. their 'boldness' (Réale et al., 2007; Bell et al., 2009), these traits may play a crucial role in the collective behaviour and functioning of animal groups.

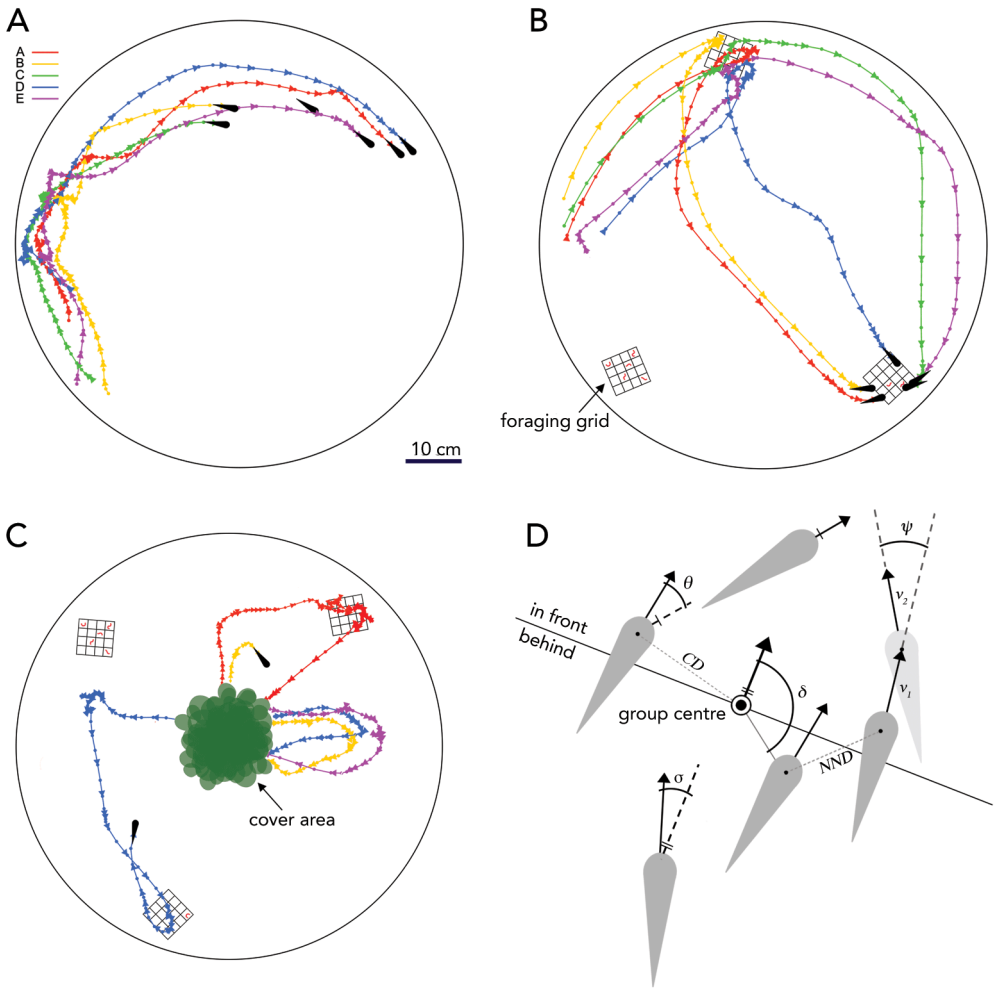

Figure 6.1 Extracting detailed individual and group movement data. Schematics of the (**A**) classic context, without food or cover, (**B**) the foraging context, with patches of food, and (**C**) the cover context, with patches of food as well as cover, with tracking segments shown for one randomly selected group. Letters refer to fish identity for which the boldness and sociability type was known. Dots indicate every 0.25s and triangles point in the direction of motion. (**D**) Graphic illustrating the spatial and movement measures acquired for each individual and for the group, with arrows depict movement vectors. For details, see the supplementary material.

To answer the question of how personality variation might affect collective behaviour, we studied the collective behaviour of free-swimming shoals of tagged three-spined sticklebacks (*Gasterosteus aculeatus*). Fish were first individually tested on sociability (attraction to other) and boldness (wiliness to take risks) before repeatedly subjecting them in groups of random composition (25 groups of 5 fish) to a large circular tank. To properly determine the mechanisms and functional consequences of personality effects on collective behaviour, we tested each group in three ecological contexts: an empty homogeneous environment, the classic collective context (e.g. Katz et al., 2011; Gautrais et al., 2012), a context with patches of food,

and a context with patches of food as well as shelter (Figure 6.1). Using custom-written tracking software (by J.W.J) we acquired individual-based high-precision tracking data and quantified detailed spatial and movements characteristics as well as foraging measures linked to each individual and each group (Supplementary Material; Figure 6.1).

Methods

Experimental system

We collected three-spined sticklebacks (*Gasterosteus aculeatus*) during the summer of 2014 from a small branch of the river Cam (Cambridge, UK) and kept them in controlled laboratory conditions (temperature: 14°C; photoperiod: 12h:12h light:dark. The wild stock of sticklebacks lived in large glass tanks (120 cm length × 60 cm width × 60 cm high) that contained dechlorinated, recycled fresh water, artificial plants and shelter, and were maintained by under-gravel and external filtration. During this pre-experimental period, the fish were fed defrosted bloodworms (*Chironomidae* larvae) *ad libitum* once daily. After an acclimatisation period of six months, when fish were about nine months old, we randomly selected 125 fish from the stock tanks and housed them in individual compartments (day 1 of the experimental period). We used 16 custom holding tanks (85 cm × 18.5 cm × 20 cm), each divided lengthwise into nine compartments (18.5 cm × 9.5 cm), eight of which were used to house individual fish, and the remaining one for an internal filter. Compartments were lined with gravel, divided by perforated transparent Perspex partitions, and contained one artificial plant each for cover. Individuals used in the experiments were size-matched (mean ± SE: 40.6 ± 0.4mm from tip of snout to caudal peduncle) to remove body size as a potentially confounding variable cf. (Harcourt et al., 2009; Webster et al., 2009). Since it is impossible to non-invasively sex sticklebacks outside the breeding season, all groups were assumed to be of mixed sex. Group sex ratio was unlikely to impact our results because of the temperature and light conditions (Borg et al., 2004), under which sticklebacks of both sexes are non-territorial and actively shoal together (Wootton, 1984).

Experimental procedure

Three days after individual housing, to control for social modulating and acclimatization effects (Chapter 3; Biro, 2012), we started with personality testing. We assayed each individual fish for boldness on experimental days 4 and 8, and sociability on days 6 and 10. After personality testing, we randomly allocated individuals to 25 groups of five fish. Grouped fish never came from the same individual housing tank to control for familiarity effects. For individual identification in the groups, after two rest days (day 13), we tagged fish individually on their middle dorsal spine with a uniquely coloured disc-shaped tag (5 mm) made from

electrical tape. Tagging took between 15-30 sec per fish and no diminished welfare was observed afterwards. This non-invasive tagging method has no effect on the activity and shoaling behaviour of three-spined sticklebacks (Webster & Laland, 2009). After a rest day, we started with the shoaling experiments using two large circular tanks (Fig. 1A). On day 15 we tested groups in the tanks without food or cover ('open context'), on day 16 and 17, twice per day, with patches of food ('foraging context'), and on day 18 and 19 with patches of food as well as plant cover ('cover context'). After each shoaling trial, fish were returned to their individual housing compartment until the next group trial. During the experimental period, fish were food deprived and individually fed three bloodworms at the end of each day (see Chapter 1). Animal care and experimental procedures were approved by the Animal Users Management Committee of the University of Cambridge, and research adhered to the Association for the Study of Animal Behaviour Guidelines for the Use of Animals in Research.

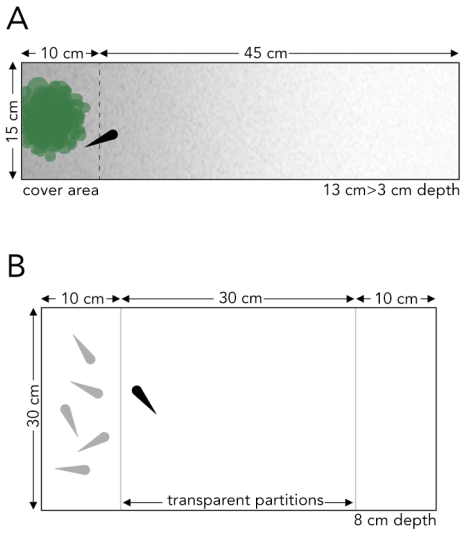

Figure 6.2 Schematics of personality assays. (A) Boldness tank with a deep area containing cover and an increasingly shallow open area. **(B)** Sociability tank with a large centre compartment in which the focal fish is placed, and two side compartments, one of which is randomly selected each four trials to house five conspecifics.

Personality testing

Individuals (n = 125) were tested in standardised personality assays (Chapter 1-5; Wright & Krause, 2006) that allowed eight fish to be tested simultaneously. To assess the 'boldness' of the fish, we placed each fish individually in a white Perspex tank (55 cm × 15 cm × 20 cm) that contained a deep, safe area with an artificial plant for cover (15 cm × 10 cm; 13 cm depth), and an open sandy area with a slope leading to shallow water (3 cm) at the other side (Figure 6.2A). Risk-taking behaviour was quantified as the amount of time an individual spent out of cover during the 30-minute trial.

To assess the sociability of the fish, we placed fish individually in the larger middle compartment (30 cm width) of a tank (50 cm × 30 cm, 8 cm depth) that was lengthwise divided by two transparent partitions to create two smaller side compartments (10 cm width), one of

which contained five conspecifics (Figure 6.2B). Sociability was quantified by measuring the average distance from the compartment containing the conspecific shoal during the 15-minute trial. The fish forming the conspecific shoal were randomly selected from the stock tanks and allowed to acclimatise to the compartment for 45 min at the start of each day. The position of the compartment housing the five fish was randomly selected every four trials, after which the shoal was allowed to acclimatise for 10 min before the start of the next trial. Different fish were used for the conspecific shoal in each of the eight test tanks and for each day.

To minimise disturbances from outside the tanks, and to standardise light levels, each tank was positioned inside a wooden test box (60 cm × 50 cm × 50 cm) and contained one LED light (Daffodil, England). For the boldness tank, the light was positioned at an angle at the covered area to create decreasing light levels with the depth of the tank; for the sociability tank, the light was positioned next to the central compartment shining upwards. Personality testing sessions were filmed at 12 fps using Raspberry Pi computers (Raspberry Pi Foundation, UK) positioned on top of each box. When not used for experiments, the water inside the experimental tanks was aerated using air stones.

Shoaling experiments

For the shoaling experiments the groups of fish were repeatedly subjected to one of two identical white Perspex tanks (80 cm diameter, 20 cm height; 7 cm depth; Figure 6.1). For the foraging context we placed three foraging patches at random locations in the tank, between 5 cm from the wall and 15 cm from the centre. For foraging patches, we used white Perspex grids (5 cm × 5 cm × 1 cm) that contained five bloodworms randomly distributed among its 16 cells. Fish were able to see the prey items at a position of approximately 15 cm from the foraging grids. For the cover context, in addition to the foraging patches, a large artificial plant was positioned in the centre of the tank to create a covered area with a diameter of 15 cm. The tanks were positioned inside a large white light tent (200 cm × 100 cm × 160 cm) to minimise outside disturbances and control light levels.

Each group received seven test trials, one in the open context without food or cover, four in the foraging context with patches of food available, and two in the cover context with patches of food as well as cover available. The order of testing and tank used were randomised for each session, but the order of contexts was fixed as not to confound the behaviour of the fish in in the classic context with foraging motivations and that in the open foraging context with the motivation of individuals to search for cover. All open context and foraging trials lasted five min while cover context trials lasted 10 min to allow enough time for the groups to deplete the foraging patches. An additional 25 min of data was recorded for each group during the classic context trials to properly calculate density maps and interaction rules for the average fish (see Figure 6.5).

For each trial, we gathered the five fish from each group from their individual compartments using a dip net and temporarily placed them in a black plastic cup. After 30 sec acclimatization, we placed all fish were simultaneously in a transparent Perspex cylinder (10 cm diameter) positioned in the centre of the tank. After another 30 sec acclimatization, the fish were released by slowly raising the cylinder using a metal crane from outside the light tent. At the end of each trial, we placed all fish back in their individual compartments, removed any droppings or uneaten prey items, and circulated the tank water to mix any potential chemical cues. All trials were filmed from above at 24 fps using Raspberry Pi computers (Raspberry Pi Foundation) at a resolution of 1400 × 1400 pixels.

As groups received two foraging trials per day with five bloodworms per foraging grid, hypothetically, a fish could have consumed 30 prey items in a day in the case it would outcompete all its group mates in both foraging trials for all food items. This was never observed. Furthermore, individual sticklebacks are capable of consuming up to 60 bloodworms within a three-hour timespan (Chapter 2). Satiation is thus unlikely to have an effect on foraging performances.

Data collection

We acquired highly detailed movement data (described below) for each fish, both for the personality trials and the group shoaling trials, using custom-written tracking software (written by J.W.J) based on Python (version 2.7.5) and the OpenCV library. For the personality trials, video images were converted to grey scale and a background image, created by averaging 200 frames, was subtracted from each frame. We identified fish via tresholding and determined their geometric centre, based on constant threshold values that were determined using pilot experiments. For the shoaling trials, we automatically identified fish from their differently coloured tags. Individual x and y coordinates in pixels were converted to mm and subsequently smoothed using a Savitzky & Sgolay smoothing filter (c.f. Herbert-Read et al., 2011) with a window of 31 frames, after which we down-sampled our data from 24 to every 4 frames to further remove any small spurious changes in position. After tracking, all trajectory data was visually checked for any inconsistencies or errors and manually corrected. For the boldness trials we used the positional coordinates to calculate the proportion of time fish spent out of cover, and for the sociability trials to calculate the average distance from the compartment housing conspecifics. For the shoaling trials we used the detailed individual positional data (24 fps at a mm-scale) to compute a range of individual and group measures (described below). Foraging data from the foraging and cover trials was acquired by manual video observations. We recorded the time each prey item was eaten (0.1 sec precision) and the identity of the forager for a total of 2646 foraging events.

Computation of shoaling measures

For each time step *t*, we calculated the group centre position (x_{gr}, y_{gr}) based on the x and y positional coordinates of all fish in the group:

$$x_{gr}(t), y_{gr}(t) = (\sum_{i=1}^{5} x_i(t), \sum_{i=1}^{5} y_i(t)) \cdot \frac{1}{5}$$

In turn, for each individual and the group (centre) we calculated its instantaneous velocity $v(t)$ (cm/sec)

$$v(t) = \sqrt{\langle x(t+1) - x(t)\rangle^2 + (\langle y(t+1) - y(t)\rangle^2} \cdot fps \frac{1}{10}$$

and heading $\psi(t)$ with respect to the positive y-axis

$$\psi(t) \; = \; \text{atan2}(x(t+1) - x(t), y(t-1) - y(t)).$$

In addition, for each individual we calculated their speeding force $a(t)$ and turning force $\alpha(t)$ (c.f. Herbert-Read et al., 2011; Katz et al., 2011), where care is taken to compute the correct angular difference with regard to the periodicity of $\psi(t)$:

$$a_i(t) = v_i(t+1) - v_i(t)$$
$$\alpha_i(t) = \psi_i(t+1) - \psi_i(t)$$
$$\{\alpha_i(t) < \; -180\}: \alpha_i = 360 - |\alpha_i(t)|$$
$$\{\alpha_i(t) > 180\}: \alpha_i = \big(360 - \alpha_i(t)\big) * -1$$

Next, we quantified the relative positioning of the fish, and calculated individual's distance to the group centre

$$CD_i(t) = \sqrt{\langle x_i(t) - x_{gr}(t)\rangle^2 + \langle y_i(t) - y_{gr}(t)\rangle^2},$$

and to their nearest neighbour $NND_i(t)$. We then calculated the angle between the positive y-axis through the group centre and an individual's position

$$\delta(t) \; = \; \text{atan2}\langle \mathrm{x}_i(t) - \mathrm{x}_{gr}(t), \mathrm{y}_i(t) - \mathrm{y}_{gr}(t)\rangle \, ,$$

and determined individual's relative heading to that of the group $\sigma(t)$ using the group's heading ψ_{gr}:

$$\sigma_i(t) = \langle \delta(t) - \psi_{gr}(t)\rangle \frac{180}{\pi}$$
$$\{\sigma_i(t) < -180\}: \sigma(t) = \; 360 - |\sigma(t)|$$
$$\{\sigma_i(t) > 180\}: \sigma(t) = \langle 360 - \sigma(t)\rangle - 1$$

In the same way we calculated the relative heading of each fish to that of their group mates θ_{ij}. Based on the relative heading and distance to the group centre, we then computed relative

coordinates for each individual, with the group centre at the origin and its heading aligned with the positive y-axis:

$$(\mathrm{xrel_i(t)}, \mathrm{yrel_i(t)}) = \mathrm{CD_i(t)}\,\langle \sin\langle\tfrac{\sigma_i(t)\pi}{180}\rangle, \cos\langle\tfrac{\sigma_i(t)\pi}{180}\rangle\rangle.$$

As a measure of group cohesion, for each time step we calculated the average inter-individual distance

$$IID_{gr}(t) = \sum_{i=1}^{5} \sqrt{\langle x_{gr}(t) - x_i(t)\rangle^2 + \langle y_{gr}(t) - y_i(t)\rangle^2} \cdot \frac{1}{5}$$

and the average individual distance to the group centre $CD_{gr}(t)$ (c.f. Delcourt & Poncin, 2012; Herbert-Read et al., 2012). In addition, we calculated the polarisation of the group $\rho(t)$, which is a measure of alignment of the fish, and ranges from -1 (complete non-alignment) to 1 (complete alignment):

$$\rho(t) = \sqrt{\sum sin(\psi_i(t))^2 + \sum cos(\psi_i(t))^2} \cdot \frac{1}{5}$$

Next, we calculated individual scores and group scores for each trial: individual median velocity v_i, average nearest-neighbour distance $\overline{NND}_i$, average centre distance $\overline{CD}_\iota$, proportion of time spent in front of the group centre ι_i (c.f. Couzin et al., 2002), group median velocity v_{gr}, group average inter-individual distance $\overline{IID}_{gr}$, group average centre distance $\overline{CD_{gr}}$, and group average polarisation $\bar{\rho}$. Furthermore, for each trial we calculated the proportion of time a group was schooling, swarming or non-cohesive. A group was defined to school when fish swam faster than half a body length (BL) per second, were relatively cohesive ($IID_{gr}(t) \leq 5$) and relatively polarised ($\rho_{gr}(t) \geq 0.6$), with empirically determined values based on the distribution of group movements. A group was defined to swarm when relatively cohesive ($IID_{gr}(t) \leq 5$) but not moving faster than 0.5 BL/sec and/or its polarisation being less than 0.6.

In addition to above positional and movement measures, for the foraging and cover context trials we also used the positional data to determine each individual's distance from the foraging grids, the proportion of time in the vicinity of (≤ 0.5 BL) and above the foraging grids, and calculated the order that individuals arrived at each of the foraging grid. Finally, for the cover context trials we used the positional coordinates to measure the proportion of time individuals spent out of cover, the proportion of time individuals spent out of cover alone, their average distance from cover, and their average order number for leaving plant cover. In turn, these measures were used to calculate the average number of fish out of cover and the proportion of time all fish were out of cover.

Data analysis

Data were analysed in R 3.0.2. We determined the consistency repeatability of risk-taking and sociability behaviour using Analyses of Variance with normalised data (Nakagawa &

Schielzeth, 2010). Significance and confidence intervals of repeatability was calculated by running 10,000 permutations of each test. Boldness and sociability scores were calculated for each fish by averaging their behaviour across both trials. Sociability scores were normalised with a Box-Cox transformation. Personality scores were scaled from 0 to 1, ranging from the least to the most sociable and the shyest to the boldest individual respectively. Body size was not linked to sociability (r_s = -0.08, p = 0.390) or boldness (r_s = 0.08; p = 0. 402), and was not significant in any further analyses ($p > 0.100$). For analyses in which we compared bold and shy or sociable and non-sociable fish, we used the third highest and third lowest scoring individuals respectively (c.f. Wilson, 1998; Ward et al., 2004).

We used a linear mixed modelling approach (Crawley, 2007; Magnhagen, 2012) to investigate the role of boldness and sociability in individual and group shoaling and foraging measures. Separate models were run for the three different shoaling contexts. Models of individual-level measures included boldness, sociability, and the interaction between them as fixed effects, and group as a random factor to account for the non-independence of individuals within a group. For the foraging and cover contexts, individual was added as an additional random factor nested in group to account for the repeated measures nature of the data. The models of group-level behaviour included average boldness of the group, average sociability, and the interaction between them as fixed effects. Group was included as a random factor to account for the repeated measures nature of the data for the foraging and cover contexts. Minimal adequate models were obtained by backward stepwise elimination (i.e. sequentially dropping the least significant terms from the full model, until all terms in the model were significant) following Crawley (2007). Statistics for non-significant terms were obtained by adding the term to the minimal model. Residuals were visually inspected to ensure homogeneity of variance, normality of errors and linearity. If assumptions were violated, data were log-transformed. All data were fitted to a Gaussian error distribution except for the number of prey items eaten, which was fitted to a Poisson error distribution with log link function, appropriate for count data.

To investigate how individuals' sociability was linked to the initiation and response to changes in behaviour, we used cross-correlation (Krause et al., 2000; Katz et al., 2011) to test how strongly the direction and speed of the most sociable fish in each group was correlated with the speed and direction of the least sociable fish in the group. We compared the speed and direction of the fish up to 50 frames (~2 sec) earlier and later, in time steps of 1/24th of a second. By determining the time point for the maximum correlation coefficient for each pair, we thus quantified which fish predominantly led the other. To determine if individual behaviour was repeatable across the free and foraging contexts we used linear mixed models with individual ID as a random factor. To determine the repeatability of behaviour we used Analyses of Variance and, if needed, scaled data to account for any group-level effects between the contexts (Nakagawa & Schielzeth, 2010). We excluded one open context trial because one

individual had a nearest-neighbour distance more than 5 standard deviations from the group average. One fish died before the fourth foraging context trial, leading us to exclude that group from then onwards. Finally, due to a recording error, analyses on the foraging measures excluded one group that could not be scored during the two cover context trials. All results $0.10 > p > 0.05$ are reported as trends and $p < 0.05$ as significant. Means are quoted ± SE throughout.

Results and discussion

Large and repeatable inter-individual differences were revealed in both boldness (R = 0.48 [95% CI: 0.34-0.62]) and sociability (R = 0.56 [0.44-0.68]), with no correlation between the traits (r_s = -0.05, p = 0.558; Figure 6.3A). The random groups contained a large variability in group compositions, both in terms of the group mean personalities as well as the range of scores in each group (Figure 6.3B).

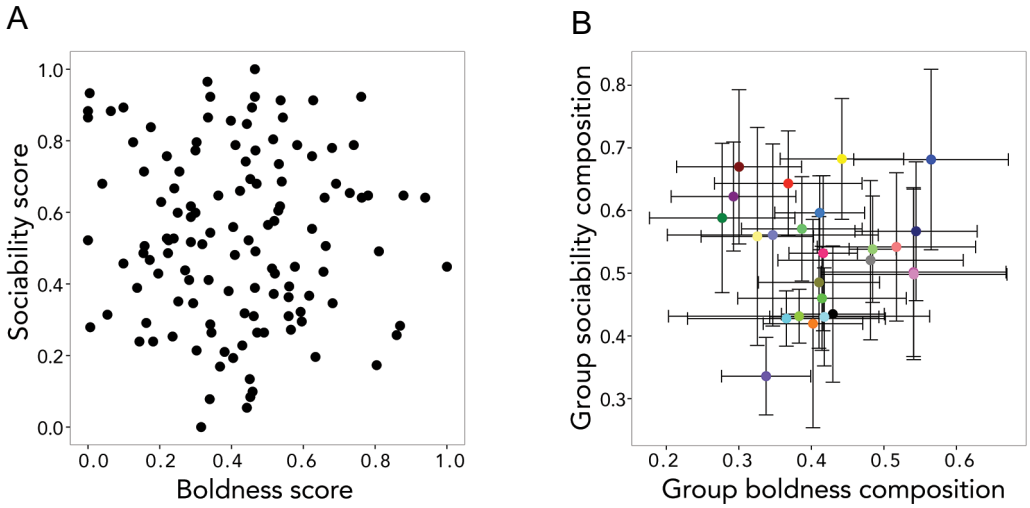

Figure 6.3 Individual and group personality scores. (A) No correlation between boldness and sociability. Personality scores (n = 125 fish) were based on the average proportion of time spent out of cover (boldness) and the average distance from the conspecific compartment (sociability). Scores were normalised and scaled from 0 to 1, with high scores indicating more sociable and bolder individuals. **(B)** Variability in group personality composition. The 25 groups of five randomly selected fish, varied considerably in their composition of boldness and sociability types. Shown are group mean personality scores (coloured dots) with standard errors depicting the range of both personality types.

In the classic collective context, sticklebacks maintained on average clear zones of attraction and repulsion by changes in their relative speeding and turning forces (Figure 6.4) in high accordance with work on other species and group sizes (Herbert-Read et al., 2011; Katz et al., 2011), highlighting the effectiveness of interaction rules in driving collective behaviour. However, variation in sociability had a strong effect on the behaviour of individual group members and the groups as a whole. More sociable individuals had smaller nearest-neighbour

distances (LMM: $\chi^2_1 = 25.87$, $p < 0.001$) and more central group positions ($\chi^2_1 = 33.20$, $p < 0.001$; Figure 6.5A). As a result of the variability in social attraction in the group, over time relatively less sociable individuals ended up predominantly in the front of the group (5 min: $\chi^2_1 = 4.23$, $p = 0.040$; 30 min: $\chi^2_1 = 7.92$, $p = 0.005$; Figure 6.5B). Cross-correlations (Krause et al., 2000; Couzin & Krause, 2003) revealed that speed and turning changes propagated from the least to the most sociable individual (Figure 6.6), indicating that leadership may emerge as a result of variability in social attraction, supporting theoretical predictions (Conradt et al., 2009).

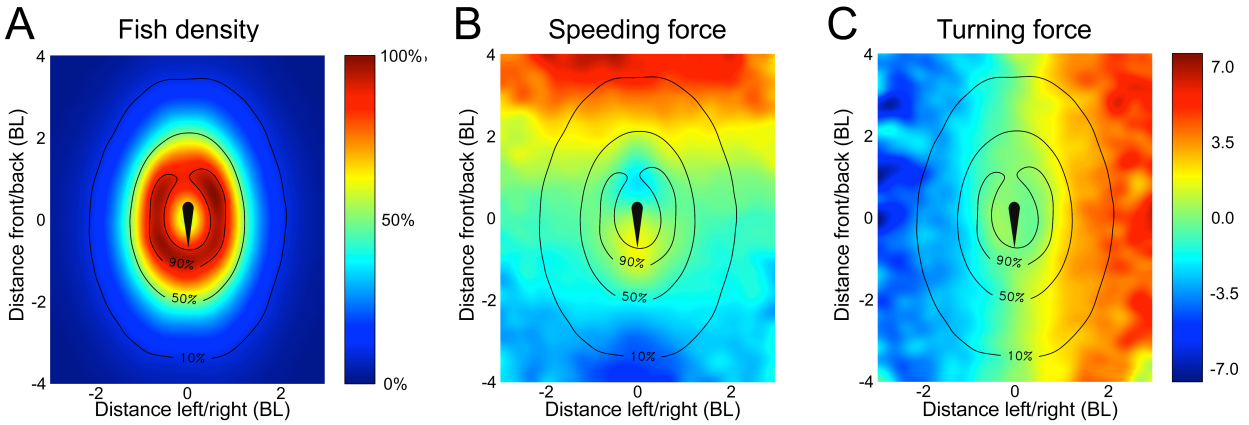

Figure 6.4 Heat maps of the density, speeding force, and turning force of the average fish in the open context. Using custom tracking software we determined the individual positions of all fish and, in turn, selected each fish in each group as the 'focal fish', placed it at the origin pointing north, and measured the relative position and heading of its group mates. Heat maps show **(A)** the probability of finding the neighbouring fish at a given position relative to the position of the focal fish, as well as the **(B)** speeding and **(C)** turning components of the mean measured effective force on the focal fish as a function of the position of its group mates (see supplementary material), following Katz et al. (2011). Data is based on the full 30 min open context trial. Distances are expressed in units average body length (BL). Fish density is presented in percentages relative to the densest bin. Speeding and turning forces are presented in the same colour scale: for speeding forces, positive values indicate speeding up and negative values slowing down; for turning forces, positive values indicate a right turn and negative values a left turn. Focal fish were less than four body lengths in front or behind and less than 2.5 body lengths left or right of their four shoal mates for 98.9% of the time. These plots show that fish are very likely to be within one body length of a neighbouring fish side-by-side, and within 2 body lengths front-to-back. Furthermore, fish sped up when the neighbouring fish were far ahead or just behind them, but slowed down when far behind or just in front of them. And also, fish turned left when the neighbouring fish was on the far left side of the fish and turned right when the fish was on the far right side of the fish, with slight opposite turning tendencies when neighbouring fish were very close.

These individual-level effects also had major driving effects on group characteristics: groups composed of more sociable individuals were more cohesive ($r_s = 0.66$, $P < 0.001$) but less polarised ($r_s = 0.46$, $P = 0.02$) and travelled less far ($r_s = 0.59$, $P = 0.002$) than less sociable groups. Group sociability composition thus had a strong effect on the tendency of groups to school (see Delcourt & Poncin, 2012), with less sociable groups mostly schooling but highly sociable shoals predominantly swarming ($r_s = 0.56$, $P = 0.003$; see Figure 6.5C). These results highlight that differences in alignment can simply emerge from variability in social attraction

(Katz et al., 2011), confirming theoretical predictions (Couzin et al., 2002). In contrast to sociability, in this context with relatively homogenous risk-reward trade-offs, boldness did not have any influence on the positioning and movements of individuals or groups ($p > 0.300$).

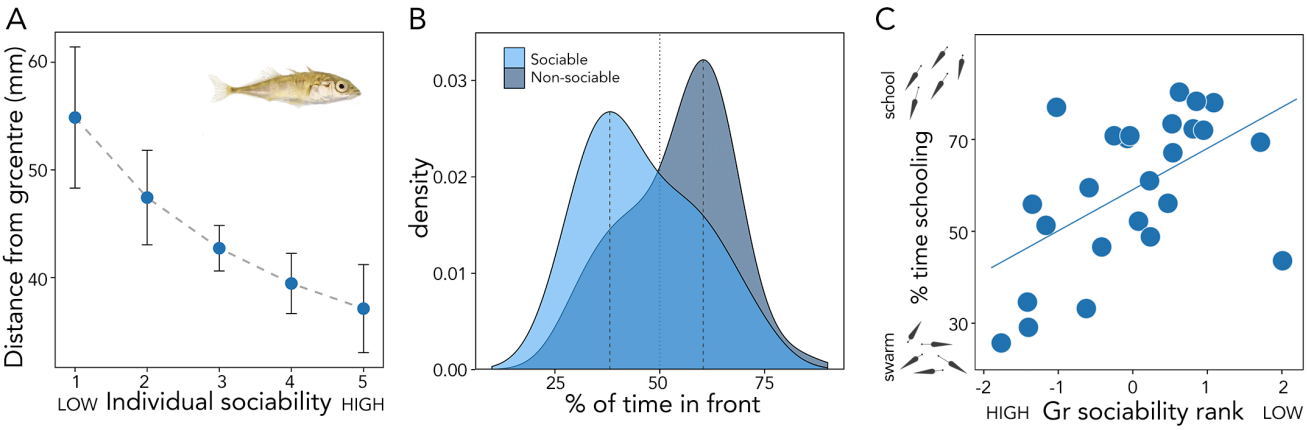

Figure. 6.5 Sociability drives individual behaviour and group characteristics. In the classic context, (**A**) sociable fish had more central positions in the group, while (**B**) relatively less sociable fish spent more time in front of the group. Density plot depicts the fish that were the third least and third most sociable relative to their group mates. (**C**) The proportion of time groups schooled, i.e. moving at least 0.5 body length/sec, cohesive ($IID_{gr}(t) \leq 5$), and relatively polarised ($\rho_{gr}(t) \geq 0.6$), was negatively linked to sociability composition: more sociable groups predominantly swarmed while non-sociable groups predominantly schooled.

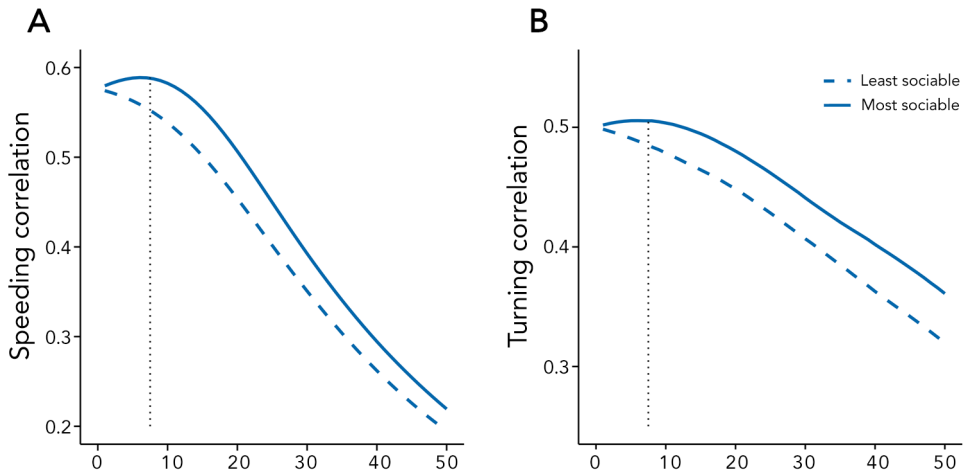

Figure 6.6 Propagation of speed and turning changes. Temporal correlations in speed and turning between the least and most sociable individual in each group (n = 25), calculated by cross-correlation (Bumann & Krause, 1993; Krause et al., 2000; Katz et al., 2011). We compared the speed and heading of the most sociable fish with that of the least sociable fish in each group up to 50 frames earlier and 50 frames later (~ 2 sec) on the full 24 fps data (x-axis). Subsequently, for each comparison we calculated the Pearson correlation coefficient. Curves show median correlations for the most sociable fish with respect to the least sociable fish (solid line), and for the least sociable fish with respect to the most sociable fish (dashed line). Analysis was restricted to frames in which fish were between 1 and 4 body lengths apart (c.f. Katz et al., 2011). For the most sociable fish, both the speed correlation (**A**) and the turning correlation (**B**) peaked after zero, with a delay time of approximately 0.3 sec (8 frames) before decaying, whereas for the least sociable fish, the correlations do not show a peak after 0. These results suggest that the most sociable individuals speed up, slow down and turn in response to the speed and heading of the least sociable individual (Bumann & Krause, 1993; Katz et al., 2011).

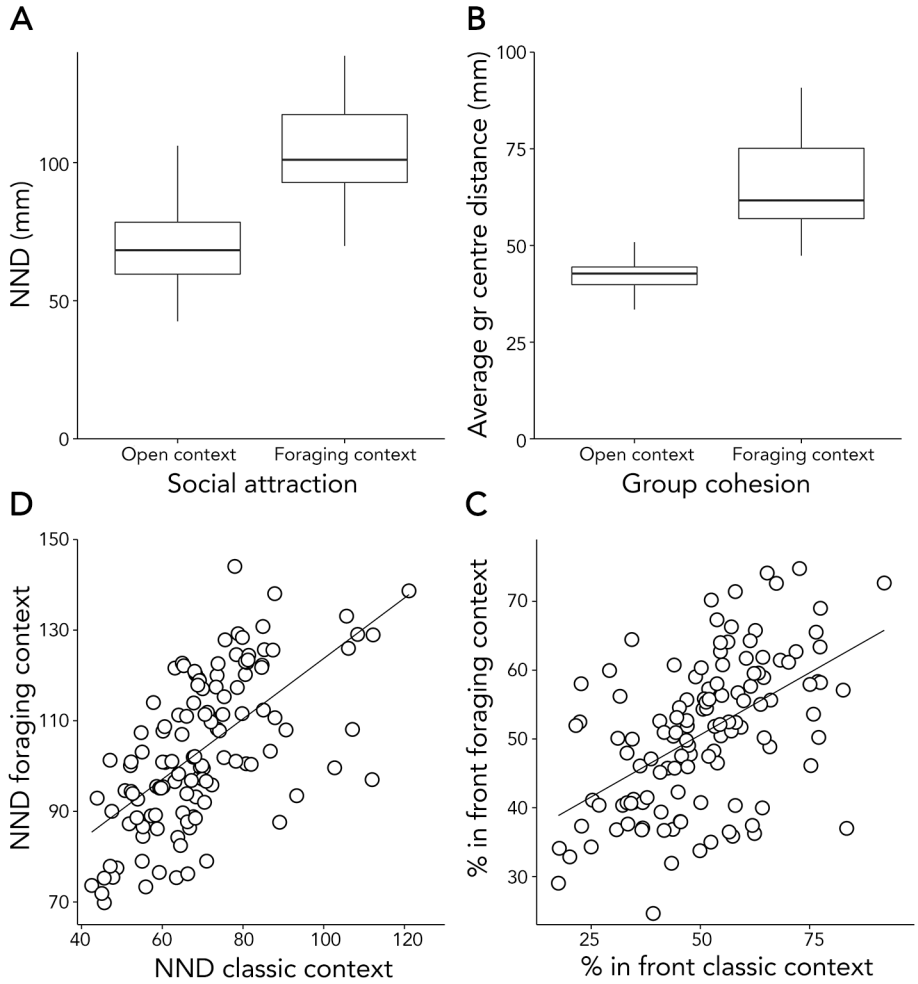

Figure 6.7 (**A** and **B**) Standard boxplots with upper and lower hinges corresponding to the first and third quartiles, of individual's average nearest neighbour distance (**A**) and group cohesion in terms of the average individual centre distance of groups (**B**) when tested in the open and foraging context. (**C** and **D**) Behavioural consistency of individuals when tested in the open context and the foraging context in terms of their average nearest neighbour distance (**C**) and the % of time in front of the group (**D**).

Next we tested groups in the same context but now with patches of food available (Figure 6.1B), thus introducing a clear goal that the fish can pursue with potential rewards. Due to the patchiness of food, individuals engage in scramble competition (Ward et al., 2006; Webster et al., 2009) and producer-scrounger dynamics may emerge linked. Relative to the homogeneous context, individuals had much larger nearest-neighbour distances ($\chi^2_1 = 324.65$, $p < 0.001$; Figure 6.7A) and formed looser shoals ($\chi^2_1 = 92.30$, $p < 0.001$; Figure 6.7B), as often seen in foraging animals (Ryer & Olla, 1998; Hoare et al., 2004). Nevertheless, behavioural differences between individuals were highly repeatable between the two contexts (nearest-neighbour distance: $R = 0.60$ [0.49-0.72], Figure 6.7C; % time in front: $R = 0.49$ [0.36-0.63], Figure 6.7D).

Linked to their spatial positioning and leadership, less sociable individuals were more likely to independently encounter the foraging patches ($\chi^2_1 = 11.94$, $p < 0.001$), but also varied more in their order of arriving (var test: $F_{41,\ 40} = 0.42$, $p = 0.007$). In contrast, relatively sociable

individuals were more likely to scrounge, and remained at the foraging patches for longer (χ^2_1 = 8.38, p = 0.004). Although bolder fish were not earlier to arrive at the foraging patches than shyer fish (χ^2_1 = 3.16, p = 0.075), they were much quicker to feed (χ^2_1 = 7.28, p = 0.007), and spent more time at the foraging patches (χ^2_1 = 10.86, p < 0.001). As a result of these complementary effects of both traits, the foraging success of individuals was determined by the combination of their boldness and sociability type (χ^2_1 = 5.62, p = 0.018; Figure 6.8A): although bold non-sociable fish had the highest food intake, fish that were shy had higher food intake when they were relatively more sociable. Also across the groups with different personality compositions, more sociable fish had more stable, intermediate levels of food intake (var test: $F_{41,\ 40}$ = 0.45, p = 0.012; Figure 6.9A), in line with theoretical predictions related to the uncertainty of leadership (Johnstone & Manica, 2011). When we account for the time individuals spent at the foraging grids, we still found that bolder individuals had much higher foraging rates than their shyer group mates (χ^2_1 = 11.48, p < 0.001; Figure 6.9B), highlighting that boldness is not only linked to higher foraging motivation but also higher foraging efficiency, likely the result of lower vigilance.

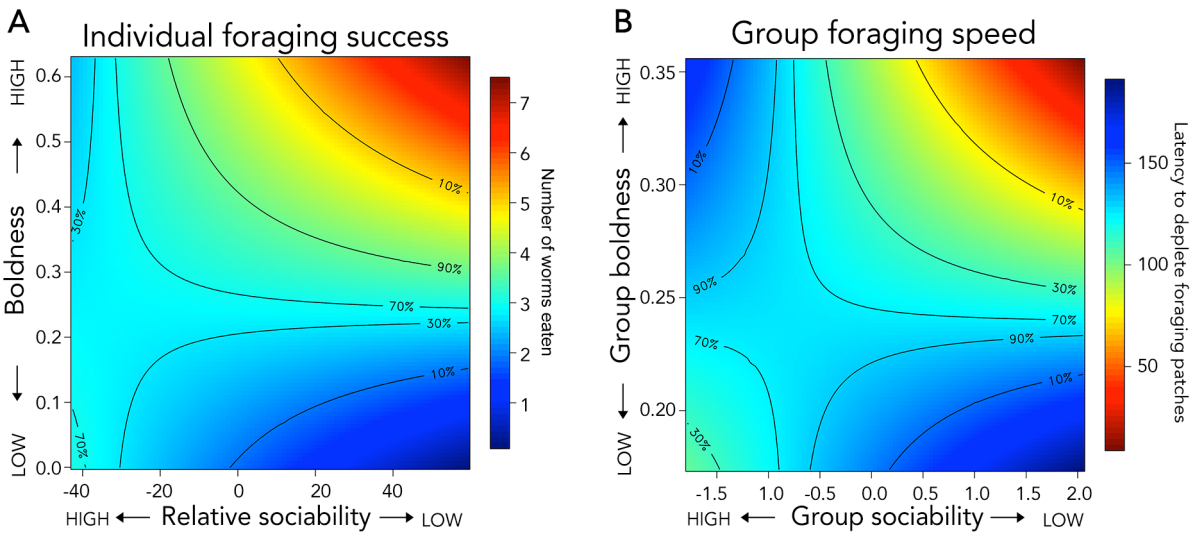

Figure 6.8 Boldness and sociability play a key role in (A) the foraging success of individuals and (B) the foraging speeds of groups (B). Bold, non-sociable individuals had the highest food intake and bold, non-sociable groups were the fastest at depleting all foraging patches. Group personalities are based on the average personality type in the group. Surface plots show a LMM fit to the data.

Linked to their strong effects at the individual level, the composition of boldness and sociability types together drove the foraging dynamics of the group (χ^2_1 = 7.58, p = 0.006): groups composed of mainly bold, non-sociable fish were the fastest to find and deplete all foraging patches, while a high sociability composition improved the foraging speed of shyer groups (Figure 6.8B). The link between foraging and group personality composition was still clear when all food had been depleted, with bold, non-sociable groups schooling the most, and

shy, non-sociable the least (χ^2_1= 9.54, p = 0.002). Because bold groups were the fastest at foraging, individuals part of such a group actually had reduced food intake (χ^2_1 = 8.16, p = 0.004). Similarly, although individuals in sociable groups may benefit from their higher cohesion, linked to lower predation risk (Pitcher & Parrish, 1993; Krause & Ruxton, 2002), their higher tendency to swarm makes them less likely to have scrounging benefits, in line with theory supporting theory (Couzin et al., 2002; Couzin & Krause, 2003).

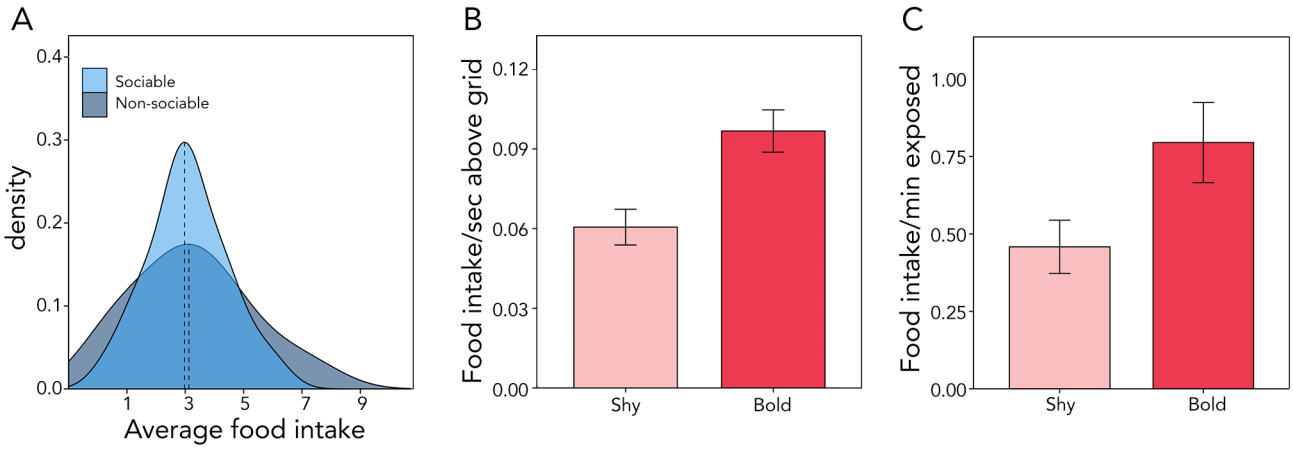

Figure 6.9 Individual personality effects on foraging. (**A**) Variance in food intake is lower among sociable fish when tested in the non-covered environment containing patches of food, showing that the stability of food intake is less affected by group composition for more sociable individuals. (**B** and **C**) Bolder fish are more efficient foragers, both in terms of their food intake relative to the time spent above the foraging grids (**B**), and the time spent out of cover (**C**).

Finally, we tested groups in a foraging environment that also included plant refuge, thus giving fish the option to search for food or hide in cover (Figure 6.1C). In this context, potential per capita risks and rewards are higher (Magurran & Pitcher, 1983) and as a result enhanced heterogeneities within and between the groups may be expected (Webster et al., 2013). Indeed, variability in individual foraging success increased considerably compared to the cover-free foraging context ($F_{124,119}$ = 0.38, p < 0.001), with only 2.56 ± 0.16 fish being out of cover on average. Both individual foraging success (χ^2_1= 8.18, p = 0.004) and group foraging speed (χ^2_1 = 6.78, p = 0.009) were again strongly linked to an interaction between boldness and sociability. But, as predicted given the availability of cover, the link between boldness and individual foraging success became much stronger (χ^2_1= 10.65, p = 0.001). Furthermore, the variance in foraging speed between the groups increased considerably, with sociable group having clear intermediate speeds (Figure 6.10). Bolder fish spent more time out of cover (χ^2_1= 12.03, p < 0.001) and more time out of cover alone (χ^2_1= 10.09, p = 0.001), explaining their higher foraging success. In the wild, however, this benefit is likely mitigated by higher risk of predation (Bell & Sih, 2007). Even when accounting for time spent out of cover, food intake rates were still higher for bolder than shyer fish (χ^2_1= 5.94, p = 0.015; Figure 6.9C), not only

highlighting their higher motivation to feed (Chapter 2; Ward et al., 2004; Ioannou, Payne & Krause, 2008), it again suggests that bold individuals are more efficient in foraging. Bold individuals were also more likely to lead their group mates out of cover ($\chi^2_1 = 10.05$, $p = 0.002$), as previously found for foraging pairs (Harcourt et al., 2009; Nakayama et al., 2013), but also to the foraging patches ($\chi^2_1 = 15.05$, $p < 0.001$). These results clearly show boldness is linked to risk-balancing (Pitcher & Parrish, 1993), with bold individuals quantitatively trading-off food value against risk while, shy individuals prioritise predator avoidance, with large effects on group foraging dynamics and the emergence of leaders and followers (Conradt et al., 2009).

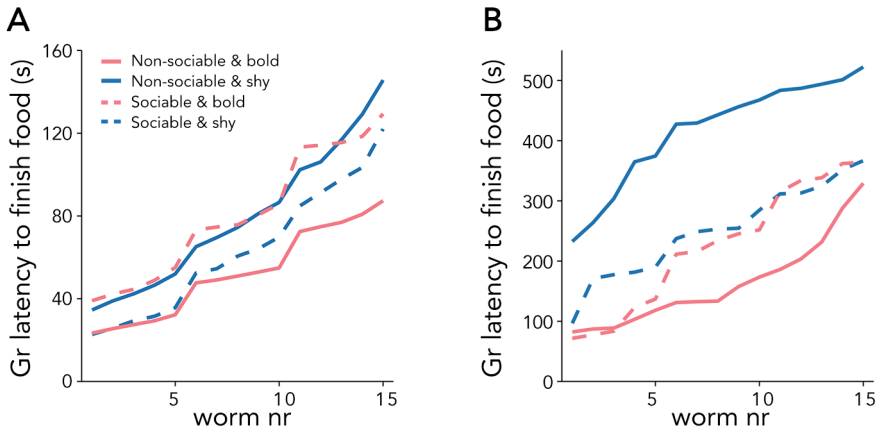

Figure 6.10 Group foraging over time. Latency in seconds from the start of the trial to finish all 15 prey items from the three foraging patches. Data shows the group average boldness and sociability compositions separate by the lowest and highest 50% of groups

Together, our results highlight that personality variation is a key driver of collective behaviour (Dyer et al., 2009a; Pruitt & Riechert, 2011a; Farine et al., 2015). Across three different contexts, sociability and boldness had strong parallel effects on the spatial positioning and leadership of individuals, in turn affected group movement characteristics, and determined group foraging. We also show that, by affecting group functioning, the group personality composition ultimately determined an individual's performance. This feedback loop between personality and group functioning may potentially lead to selection pressures on personality (see Farine et al., 2015), with the behavioural differentiation in boldness and sociability types resulting from conditional strategies in collective behaviour (Wolf & Weissing, 2010). This would provide a potential adaptive explanation for the existence of personality variation that complements existing models about state differences (Dingemanse & Wolf, 2010), responsive behavioural types (Wolf et al., 2011; Wolf & McNamara, 2013) and leader-follower polymorphisms (Conradt et al., 2009; Johnstone & Manica, 2011). It is time for a new generation of theoretical and empirical work that integrates the fields of collective behaviour and animal personality, and considers both the consequences of personality variation for collective action (Harcourt et al., 2009; Herbert-Read et al., 2012; Aplin et al., 2014) as well as its potential causal links via group formation and functioning (Wolf & Krause, 2014; Farine et al., 2015).

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Chapter 7

Concluding remarks

Over the last decade, booming interest in between-individual variability in behaviour has resulted in a broad and well-developed literature that has substantiated animal personality as a central component of the behavioural ecology of animals. A wide variety of traits, often correlated between different contexts, exist in populations across the animal kingdom. These traits are often heritable, the subject of natural and sexual selection, and have considerable implications for a large range of important ecological and evolutionary processes. Despite group living being a widespread phenomenon, current understanding of the role of animal personality in grouping animals remains relatively poor. In this thesis I aimed to develop an integrated view of personality differences in relation to the social context, using the three-spined stickleback as my model species.

First, I showed that boldness but not sociability is linked to food acquisition, even for fish at rest, laying the foundations for understanding the role of these traits in a social context (Chapter 2). Next, I showed that social experiences can carry-over and obfuscate the personality expression of individuals when alone (Chapter 3), and that via social feedback mechanisms individual's risk-taking and leadership behaviour can be modulated not only by the current but also the previous social context (Chapter 4). Further detailed observations revealed that bolder fish had lower social attraction during collective movements with a partner, modulated by social feedback, helping to explain the mechanisms underlying leadership and social coordination (Chapter 5). Finally, using an individual-based approach for a large-scale study of free-swimming shoals of fish, I showed that boldness and sociability have strong and complementary driving effects on the social structure, collective behaviour, and functioning of moving groups, and that this in turn determines individual performance (Chapter 6). In this final chapter, I synthesise the most important findings, discuss arising questions, and highlight some exciting directions for future work.

7.1 A synthesis

With the studies in this thesis I specifically aimed to provide an integrated view of animal personality in the social context. Using a multi-level approach, from motivations, social modulating effects, individual consequences of personality variation, to the driving effects of group functioning, I show personality differences and the social context are crucially linked. Personality is a key driving factor of collective behaviour and explains group functioning, yet the social context also strongly modulates individual personality expression and determines its performance. Personality variation may thus not only be a driver of collective action; the individual performance of personality types is ultimately determined by the composition of the group. This forms an important feedback loop that may potentially lead to selection pressures on personality (see Farine et al., 2015).

In this section, I create a synthesis of animal personality in relation to the social context. With a holistic viewpoint on animal behaviour, I integrate the work presented in this thesis with current knowledge on the topic, from individual motivations, to social modulating effects, personality effects in a group context, and finally group level functioning.

In daily life, animals need to constantly make decisions such as when to rest, where to forage, and what environments to avoid. Most of the behavioural decisions of animals reflect a trade-off between the risk of starvation and the risk of predation (Lima & Dill, 1990; Houston & McNamara, 1999). Although these trade-offs may fluctuate over the short-term, such as in response to energy reserves (Houston & McNamara, 1999), the personality of individuals is closely linked to how individual's make such trade-offs (Gosling, 2001; Réale et al., 2007; Dingemanse & Wolf, 2010; Sih et al., 2012). Importantly, grouping comes with anti-predator (Krause & Ruxton, 2002) and foraging benefits (Lima & Dill, 1990), such as resource exploitation (Giraldeau & Caraco, 2000), but with the cost of resource competition (Pitcher & Parrish, 1993; Krause & Ruxton, 2002). The mere presence of others affects the trade-offs individuals make and results in individuals with different personality types to conform in their behaviour (Magnhagen & Bunnefeld, 2009; Magnhagen, 2012) and converge on some common rate of expression (Herbert-Read et al., 2012; Brown & Irving, 2014; King, Williams & Mettke-Hofmann, 2015). At the same time, grouping can enhance personality differences by facilitation (Webster & Ward, 2011), for example, individuals increase their activity and risk-taking behaviour due to risk dilution effects related to grouping (Webster et al., 2007; Magnhagen & Bunnefeld, 2009). Importantly, the extent that individuals show conformity or facilitation in their behaviour often depends on their personality, such as the finding that, due to being with others, shy individuals show a much larger increase in their risk-taking behaviour than bold individuals do (Chapter 4 and 5; Magnhagen & Bunnefeld, 2009).

Also the behavioural repeatability of individuals can be affected by the modulating effects of the social context (Webster & Ward, 2011). In some cases, due to the various changes in the behaviour of individuals in a social group, repeatability may lack completely (Webster et al., 2007) and even carry over to later contexts when individuals are alone (Chapter 3). This is also important for the design of personality studies as it highlights that social housing conditions need to be evaluated. Rank order differences can also be maintained despite of changes in behaviour (see Webster & Ward, 2011), and many studies have shown that individual personalities are at least to a certain extent expressed reliably in a social context (Chapter 4 - 6; Magnhagen & Bunnefeld, 2009; Herbert-Read et al., 2012; Laskowski & Bell, 2014). Besides the mere presence of group mates, their particular personality types can also affect the an individual's expression of personality (Chapter 4 and 5; van Oers et al., 2005b; Harcourt et al., 2009; Schuett & Dall, 2009; Magnhagen & Bunnefeld, 2009), adding a further layer of complexity. For example, individuals may increase their risk-taking behaviour when grouping with bold individuals but decrease it when their group mates are relatively shy

(Chapter 4 and 5; Magnhagen & Staffan, 2005; King et al., 2015), effects that again often depend on the personality of the focal individual itself (Chapter 4 and 5). Finally, over time personality differences can even be reinforced by the social context due to positive feedback from the experience of repeated social interactions (Harcourt et al., 2009; Kurvers et al., 2009; Burns et al., 2012), even those experienced in previous social contexts (Chapter 4; Frost et al., 2007; Gómez-Laplaza, 2009), which results in higher behavioural repeatability (Laskowski & Bell, 2013; Laskowski & Pruitt, 2014).

It is clear that the social context can strongly affect the expression and repeatability of personality at a number of levels. But in what way do personality differences affect the social context? What is their role in the collective behaviour and functioning of animal groups? Although individuals can be favoured to conform in their behaviour and to coordinate their activity (Conradt & Roper, 2003; Rands et al., 2003), personality variation has a major driving role on the spatial positioning, structure, leadership, and foraging dynamics of animal groups. First of all, linked to group variability in social attraction, sociable individuals are more likely to occupy central group positions and less sociable individuals positions towards the front of the group (Chapter 6). As a result, less sociable individuals are more likely to disperse (Cote et al., 2010), lead group movements (Chapter 6), and discover foraging areas (Chapter 6; Laskowski & Bell, 2014). Due to the uncertainty of producing, less sociable individuals, which are less likely to scrounge, experience higher variance in food intake (Chapter 6). Also bolder individuals are more likely to occupy positions on the edge (Aplin et al., 2014) and leading front (Chapter 4 - 6; Ward et al., 2004; Harcourt et al., 2009; Kurvers et al., 2009) of animal groups where predation risk and foraging benefits are generally highest (Bumann et al., 1997; Krause et al., 1998; Krause & Ruxton, 2002). Linked to their spatial positioning, bold individuals are more likely to discover foraging areas (Ioannou et al., 2008), depending on the context (Chapter 6), and faster to feed (Chapter 6). In contrast, shy individuals are more likely to join others and 'scrounge' at already discovered patches (Dyer et al., 2009a; Kurvers et al., 2010b), depending on the associated risks (Jolles et al., 2013b). Furthermore, bold individuals are more motivated to forage than shy individuals (Chapter 2), spend less time being vigilant, and are more efficient in foraging (Chapter 6), resulting in a strong positive link between boldness and food intake rates (Chapter 6; Ioannou et al., 2008).

As bold individuals mainly lead group behaviour, this places pressure upon shy individuals to conform, as not doing so may result in a loss of the benefits of sociality. For example, shy individuals are more responsive to the behaviour of their group mates (Chapter 4 and 5; Magnhagen & Bunnefeld, 2009; Harcourt et al., 2010a; Kurvers et al., 2010a), have higher social attraction when exposed (Chapter 5), and have stronger social network positions (Pike et al., 2008; Dyer et al., 2009a; Aplin et al., 2013) than bold individuals. Often leadership roles emerge with bold individuals taking the lead and shy individuals mostly following (Ward et al., 2004; Harcourt et al., 2009; Kurvers et al., 2009). Intrinsic leadership is linked to boldness

due to differences in how bold and shy individuals trade off risks and rewards (Conradt et al., 2009). However, boldness may not always result in effective leadership (Johnstone & Manica, 2011) as this depends on the context. For example, leadership is not linked to boldness when risk-reward trade-offs are homogeneous or no cover is available (Chapter 6). Furthermore, it is social feedback from repeated social interactions that stabilises these social roles (Chapter 4; Harcourt et al., 2009; Nakayama et al., 2012a; Flack et al., 2013), leading to higher social coordination (Sumpter et al., 2008; Conradt & Roper, 2009) and improved group dynamics (Harcourt et al., 2009; Nagy et al., 2010; Burns et al., 2012).

Besides affecting how individuals behave within moving groups, personality differences also drive the behaviour of the group as a whole. Groups composed of mainly sociable individuals are very cohesive, but show mostly undirected swarming movements (Chapter 6), which correspond to 'selfish-herd' behaviour (Hamilton, 1971; Krause & Ruxton, 2002). In contrast, relatively non-sociable groups explore considerably more (Chapter 5 and 6), and as a consequence, are more likely to find and deplete foraging patches (Chapter 6; Laskowski & Bell, 2014). Groups composed of mainly bold individuals show lower cohesion (Dyer et al., 2009a) and coordination (Chapter 5), but are faster in discovering foraging patches than relatively shy groups (Chapter 6; Dyer et al., 2009a). Also groups with a high frequency of aggressive individuals have higher foraging success (Pruitt & Riechert, 2011a). In contrast, sometimes a mixed group composition may be the most beneficial for all its members (Dyer et al., 2009a; Pruitt & Riechert, 2011b), such as in social spiders in which both docile and aggressive individuals benefit from having a diverse group (Pruitt & Riechert, 2011b).

Finally, in some cases, keystone personality types may be the driving force of the whole group, for example, in spiders and guppies, respectively the boldest and most sociable individual determine the productivity and exploration of the group as a whole (Brown & Irving, 2014; Pruitt & Keiser, 2014). Importantly, different personality traits may work in tandem, and group functioning may ultimately be determined by the interplay between them. For example, by affecting group cohesion, leadership, and exploration, the mix of boldness and sociability types in the group ultimately determined the foraging success of stickleback shoals (Chater 6). Together, these findings highlight that group personality composition can alter the fitness consequences associated with individual personality types. For example, bold individuals are inclined to accept risks for potential higher foraging gains, but these gains are relatively reduced when they are part of a bold group; sociable individuals are inclined to be close to others, but when they are part of a highly social group they may arrive on the spatial edge of the group miss scrounging opportunities due to swarming (Chapter 6).

Together, these findings show personality and the social context are intricately linked and that animal personality is a key component of collective behaviour. It is now time for a new generation of theoretical and empirical work that further integrates the fields of collective behaviour, animal personality, and evolutionary biology and considers both the consequences

of personality variation for collective action (Sumpter, 2006; Harcourt et al., 2009; Herbert-Read et al., 2012; Aplin et al., 2014) as well as its potential causal links via group formation and functioning (Wolf & Krause, 2014; Farine et al., 2015).

7.2 An outlook

The work presented and discussed in this thesis highlights how animal personality plays a key role in the life of group living animals. Nevertheless, research on the topic is still in its infancy and there is much need and scope for further work to address important unresolved questions. In this section I discuss a selection of four promising topics that I think merit further investigation.

Social development of personality

The social context has a strong modulating effect on the personality expression of individuals, which can reduce or enhance the behavioural responses of individuals and affect their behavioural repeatability. An obvious next step is to look at the ontogeny of animal personality with a specific focus on the social environment. Research on this topic is limited (Stamps & Groothuis, 2010b), but new conceptual frameworks suggests that social interactions may be key to the emergence and development of personality traits (Bergmüller & Taborsky, 2010; Montiglio et al., 2013; Laskowski & Pruitt, 2014). A few studies have shown that stable social conditions may result in more repeatable behaviour (Wolf et al., 2011; Laskowski & Bell, 2013). However, the functional consequences of long-term social conditions have not yet been considered. In the wild, different animals may experience a large range of social conditions and live in small or large groups, homogenous or heterogeneous groups, or in conditions that are very stable or fluctuate heavily over time. Do such factors play a role in determining the sociability and boldness types of individuals later in life and do they have a determining effect on an individual's behavioural plasticity? Furthermore, how do such potential changes linked to social development translate into the social functioning of animals and in turn drive group dynamics? Answering these questions has important implications for our understanding of the mechanisms underlying personality variation and may help to properly understand the link from individual behaviour, to group functioning and stability, and ultimately population dynamics.

Influence of personality effects in relation to group size

It is clear that personality differences between group members often determine how individuals behave and thereby drive collective action. The question remains, however, how the strength of personality effects depends on group size. In the wild, animal groups vary considerably in size, with most groups ranging from a few to tens of individuals (Krause &

Ruxton, 2002; Hoare et al., 2004; Sumpter, 2010), but some extending far into the millions. Investigating the link between personality effects and group size is thus important to understand the significance of personality variation in a natural situation (Webster & Ward, 2011) and is critical to fully understand the consequences of personality variation on collective behaviour and group functioning.

Up to what group size do personality differences actually matter and how does this depend on the composition of the group? Some studies suggests that individuality in group behaviour may quickly disappear with increasing size of the group (Kurvers et al., 2011; Herbert-Read et al., 2012). However, other studies show that personality differences are still clearly expressed in moderately-sized groups (Chapter 6; Magnhagen & Bunnefeld, 2009; Laskowski & Bell, 2014) and that extreme personality types may be the single most important factor that explains the collective action of animal groups (Brown & Irving, 2014; Pruitt & Keiser, 2014). Furthermore, research has shown that collective behaviours, such as group movements between different habitats, can be initiated by a small minority of individuals and subsequently adopted by the group (Reebs, 2000; Sumpter et al., 2008; Ward et al., 2008). Although research has shown that individuals keep on using the same response rules with increasing group size (Herbert-Read et al., 2011; Katz et al., 2011), their reaction patterns do change (Gautrais et al., 2012), partly due to the fact that individuals respond differently to group mates near compared to further away (Katz et al., 2011). It may be likely that, with increasing group size, the influence of individual personality types diminishes as a result of increased conformity behaviour. If that is the case, what is the exact function of this relationship and how does this differ between different traits? Furthermore, how does the role of individual personalities in larger groups depend on the composition of the group as a whole, and to what extent do extreme personalities keep on playing a prominent role in larger groups? By tracking the collective behaviour of animal groups with known identities, and investigating the role of individual personalities in groups with increasing group size and homogeneous or heterogeneous compositions, it may be possible to extract a primary function that can be used to better predict the impact of personality differences across group living species.

Personality and individual interaction rules

A fundamental question of collective behaviour research is how large-scale patterns are generated by the actions and interactions at the individual level. A key element is that the spectacular and complex patterns of collective behaviour by many group-living animals can often be explained by individuals following simple rules (Couzin & Krause, 2003; Couzin et al., 2005; Sumpter, 2006, 2010; Herbert-Read et al., 2011; Katz et al., 2011; Gautrais et al., 2012): individuals change their speed to stay close to others but move away when they get too close, with alignment emerging from such attraction and repulsion forces. However, as highlighted

throughout this thesis, boldness and sociability both have strong driving effects on the behaviour of individuals in a group. Bold individuals are more likely to explore and occupy leading positions, but shy individuals are more responsive to the behaviour of others. Sociable individuals stay closer to their group mates and have more central group positions, while less sociable individuals are more likely to follow and are less extreme in their behaviour.

The most plausible mechanism for personality having such effects on social dynamics is that certain personality types differ in their interaction rules. For example, not only the extend but the way in which individuals are attracted towards others is likely dependent on their sociability and boldness type. Sociable individuals may be likely to respond quicker and over longer distances to the location and behaviours of their group mates than less sociable individuals, and shyer individuals may have higher intensities of social speeding and turning forces than bold individuals. Such potential personality variation in the use of interaction rules could be investigated by testing pairs of individuals with highly similar and highly different personalities in various collective scenarios, while accurately tracking their movement decisions over time. The detailed positional data can then be translated into parameters to define the interaction rules and variation therein (see Chapter 6; Herbert-Read et al., 2011; Katz et al., 2011; Gautrais et al., 2012).

Personality variation and fission-fusion dynamics

Grouping is ubiquitous among animals, from swarms of insects, to schools of fish and flocks of birds. However, for many species, group formation is actually quite a dynamic process, with group size and composition changing over time due to groups splitting and merging, also known as fission-fusion dynamics (Krause & Ruxton, 2002; Couzin & Laidre, 2009; Kelley et al., 2011). Although it is increasingly clear that personality variation is of key relevance to understanding collective behaviour and group functioning, its role in fission-fusion dynamics remains relatively unclear. Studying the organisational properties of fission-fusion societies is critical to fully understand the role of personality variation in grouping dynamics and may additionally provide important insights into population-level processes (Whitehead, 2008).

Central to such dynamics is that the fact that ecological variability drives changes in the relative costs and benefits of group membership. Larger, individuals in more cohesive groups may benefit from enhanced protection from predators, but also suffer from increased competition for food (Pitcher & Parrish, 1993; Krause & Ruxton, 2002). Both predation risk (Hamilton, 1971) and foraging dynamics, such as competition for resources and conspecific attraction (Giraldeau & Caraco, 2000; Krause & Ruxton, 2002), may therefore often shape fission-fusion dynamics and the social structure of animal groups (Ryer & Olla, 1998; Hoare et al., 2004; Kelley et al., 2011). As more sociable individuals are more likely to be closer to conspecifics, have more central group positions, and are more likely to follow (Chapter 6), sociability may be negatively linked to the likelihood of individual's to split away from animal

groups (Cote et al., 2010). Also boldness variation may play an important role in fission-fusion dynamics. Bolder individuals are more likely to explore, are less responsive to their group mates, and more likely to take the lead; shyer individuals may be more likely to remain in subgroups while bolder individuals move between them.

Some studies that have investigated social interaction dynamics are in line with these hypotheses. For example, less sociable and bold individuals have a higher tendency to disperse (Dingemanse et al., 2003; Cote & Clobert, 2007; Cote et al., 2010) and have less strong social associations that they share with a larger number of individuals (Pike et al., 2008; Croft et al., 2009; Aplin et al., 2013). In addition, bold individuals have a lower tendency to split into smaller subgroups (Michelena et al., 2008). However, the potential link between personality variation and fission-fusion dynamics has never been directly investigated. The question remains if personality differences, next to affecting individual and group behaviour, also play an important role at the population level by potential strong differential effects on fission-fusion dynamics. Furthermore, if group personality composition plays such an important role on the effectiveness of individual personality types, as described above, this raises the crucial question to what extent this is important in socially fluctuating groups? To what extent does dynamic social feedback, expected for fission-fusion societies, affect the behavioural repeatability of individuals? One potential way to investigate these exciting questions is to use a mesocosm set-up in which large numbers of individuals with known personality can roam free and interact, while their individual spatial positions and thereby fission-fusion dynamics in the environment can be accurately recorded over time, using the sophisticated tracking technology that is now available.

7.3 Concluding

The work in this thesis highlights a crucial role for personality variation in group-living species. By a series of experimental studies, I present an integrated view of the link between animal personality and the social context that exists at multiple levels. I show that personality has a key driving influence on key aspects of group functioning, including social structure, leadership, group cohesion, foraging dynamics, and collective movements. The social context and group composition thereby strongly modulate the repeatability of personality and the expression of personality, and ultimately determine individual's performance.

Although my research has a clear focus on the role and meaning of personality differences, I see my work as part of a larger research programme with the aim to create an integrated and holistic view on animal behaviour (Tinbergen, 1963; McNamara & Houston, 2009). Ultimately, by linking consistent behavioural tendencies with individual motivations and risk-reward trade-offs all the way to group functioning, we will get closer to the fundamental mechanisms that explain why animals behave as they do.

I hope that this thesis will inspire other researchers to study this exciting topic and that knowledge and insights from these new findings will be used for a more multidimensional and integrative approach to properly understand the richness of animal behaviour.

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Curriculum Vitae

Jolle Jolles was born on the 13th of February 1985 in Utrecht, the Netherlands. He graduated from the Montessori College Maastricht in 2003. In September 2007 he received his Bachelor's degree (cum laude) in biology at the University of Groningen after which he worked for 5 months as a field assistant on primate behaviour projects in Kalimantan, Indonesia, and on the Cape Peninsula, South Africa. In September 2010 he received his Master's degree (cum laude) in Neuroscience and Cognition at Utrecht University, the Netherlands, specializing in Behavioural Biology. As part of his degree, Jolle set up two behavioural studies. The first study was conducted under supervision of Dr Ruud van den Bos at the Rudolf Magnus Institute, Utrecht, and focused on the links between risk-taking behaviour, decision-making, and sex differences in rats. The second study was performed under supervision of Prof Nicky Clayton FRS at the University of Cambridge, England. This study focused on the link between dominance, affiliations, and boldness on social foraging strategies in rooks. In October 2010 Jolle started a research associate job with Dr Alex Thornton and helped establish a large-scale project to investigate intelligence and culture in wild jackdaws. In October 2012 he started a PhD in the Evolutionary Ecology Group under the supervision of Dr Andrea Manica for which he received a Biotechnology and Biological Sciences Research Council (BBSRC) scholarship. His PhD research focused on then causes and consequences of individual variation in behaviour (personality) in group-living animals. Using the three-spined stickleback as his model species, he conducted a range of laboratory experiments to investigate the mechanisms underlying personality variation, social modulatory effects on personality expression, and personality effects on collective behaviour and group functioning. In January 2016 Jolle will continue his research on animal personality and collective behaviour at the Department of Zoology, University of Cambridge as a postdoctoral researcher, and in April 2016 he will join the Department of Collective Behaviour at the Max Planck Institute Radolfzell to work as a Postdoc with Prof Iain Couzin.

Appendix

During my PhD, I worked on a couple projects that were not directly related to my thesis and which are therefore not included here, but resulted in the following publications:

Jolles, J.W., King, A. J., Manica, A. & Thornton, A. (2013). Heterogeneous structure in mixed-species corvid flocks in flight. *Animal Behaviour* **85**, 743–750.

Jolles, J. W., Ostojić, L. & Clayton, N. S. (2013) Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus*. *Animal Behaviour* **85**, 1261–1269.

van den Bos, R., Jolles, J. W. & Homberg, J. R. (2013) Social modulation of decision-making: a cross-species review. *Frontiers in Human Neuroscience* **7**.

Zandberg, L., Jolles, J. W., Boogert, N.J. & Thornton, A. (2014) Jackdaw nestlings can discriminate between conspecific calls but do not beg specifically to their parents. *Behavioral Ecology* **25**, 565–573.

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